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Department of
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Forest Service

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Station**

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Technical
Report NE-85

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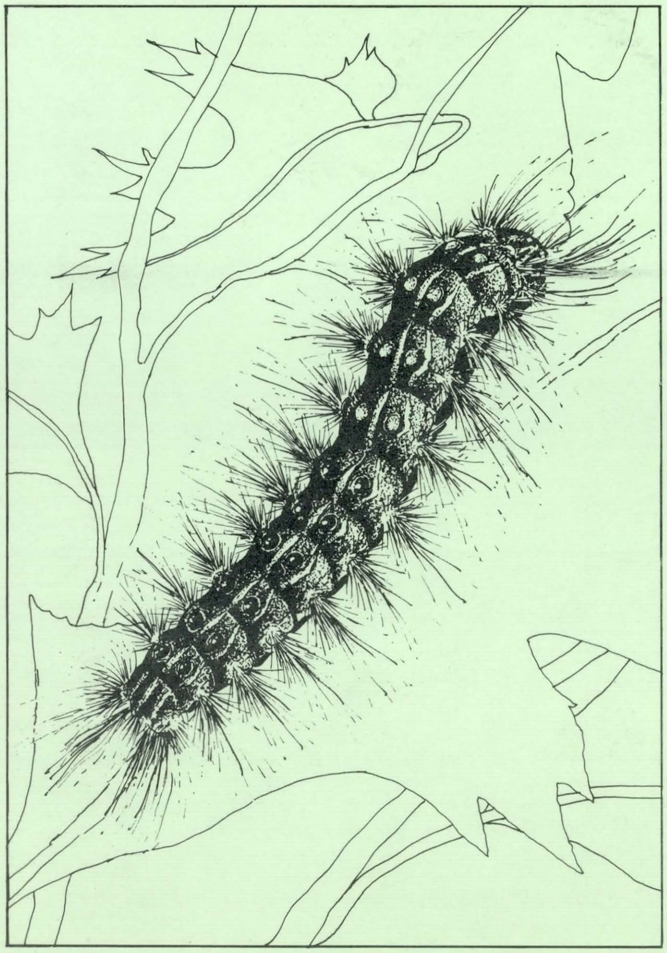
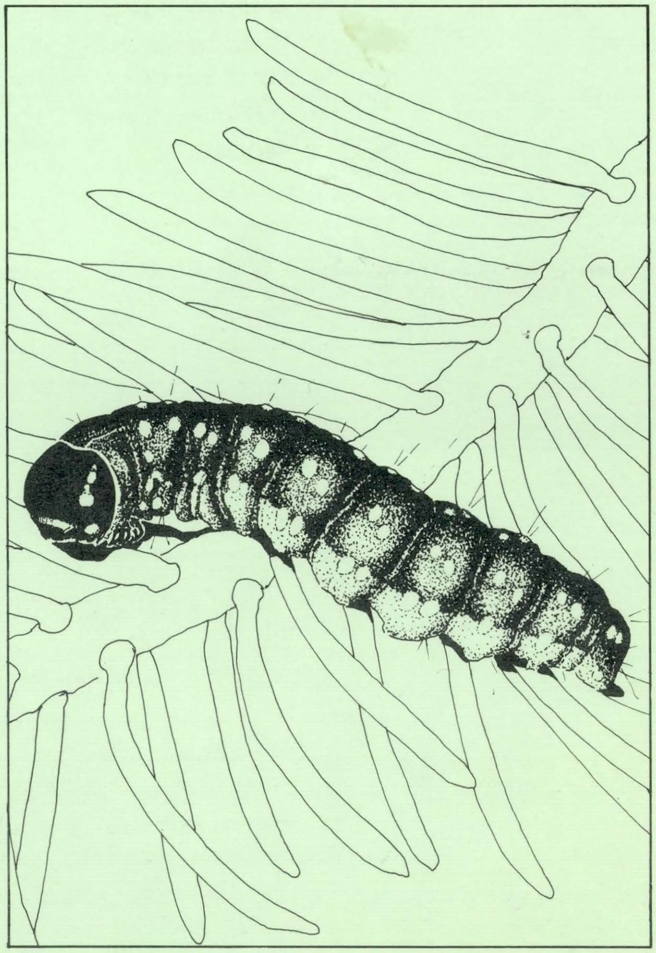
Proceedings

Forest Defoliator - Host Interactions: A Comparison between Gypsy Moth and Spruce Budworms





FOREWORD

The Canada/U.S. Spruce Budworms Program in cooperation with the Center for Biological Control of Northeastern Forest Insects and Diseases of the Northeastern Forest Experiment Station co-sponsored this Forest Defoliator-Host Interaction Workshop. This invitational workshop was limited to investigators of the spruce budworms and gypsy moth in the Forest Service, Canadian Forestry Service, and the University sector. The primary purpose of this workshop was to foster communication between researchers having a mutual interest and active research projects designed to understand the relationships between the host plant and forest defoliator feeding behavior, growth, and reproduction.

This Workshop was a follow-up to two previous meetings on host-insect interaction. In 1980, Dr. W. Mattson hosted a CANUSA-sponsored meeting at the North Central Forest Experiment Station, St. Paul, MN. This informal gathering brought together CANUSA Program investigators from the US and Canada for the purpose of sharing preliminary information and data on host-insect interactions. The second meeting took place in the fall of 1982. CANUSA(E) sponsored a Symposium on Spruce Budworm-Host Interaction at the Eastern Branch Meeting of the Entomological Society of America, Hartford, CT. The current Workshop developed from this Symposium. We found that participants were raising question concerning the similarity or differences between the spruce budworm and gypsy moth host interaction systems.

These Proceedings resulted from a three-day Workshop held in April 1983 at the Park Plaza Hotel, New Haven, CT. The structure of the Workshop allowed each participant a period for a presentation followed by lengthy discussion. These discussions were lively, friendly technical exchanges clarifying or elaborating on points raised by the speaker. Frequently, these exchanges were thought-provoking and often provided avenues for further detailed discussions and in some cases, future cooperative efforts.

The papers that make up these Proceedings were submitted at the Workshop as camera-ready copy. As a result, the participants did not have the benefit of reappraising their work in light of the discussions that followed their presentations or other ideas that developed at the Workshop.

Since the Workshop was planned late in the life of the CANUSA Program, we asked each investigator to be especially aware of the implications of these interactions on population dynamics of the insect in relation to forest management potential. When possible, we also asked that future research needs and direction be mentioned.

As technical coordinators for this Proceedings, it was our task to arrange and more effectively focus material so that papers provide a smooth transition of ideas and research activities on insect-host interactions for the spruce budworms and gypsy moth.

Lastly, we would like to acknowledge the support and confidence expressed by the following:

Denver P. Burns, Director, Northeastern
Forest Experiment Station

Melvin E. McKnight, Program Leader, CANUSA

William E. Wallner, Director's
Representative, Hamden, CT

August 1983 Robert L. Talerico, Broomall, PA

COVER SKETCH

Left, gypsy moth larva; right, spruce budworm larva.

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PROCEEDINGS,

forest defoliator--host interactions:

A comparison between gypsy moth and spruce budworms

New Haven, Connecticut, April 5-7, 1983

Technical Coordinators:

Robert L. Talerico
Research Coordinator
CANUSA(E)
Broomall, PA 19008

Michael Montgomery
Research Entomologist
Northeastern Forest Experiment Station
Center for Biological Control of
  Northeastern Forest Insects & Diseases
Hamden, CT 06514

Sponsored jointly by the
Canada/United States Spruce Budworms Program
Northeastern Forest Experiment Station

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SUMMARY OF LIFE HISTORY AND HOSTS OF THE SPRUCE BUDWORMS

Robert L. Talerico

Research Coordinator, CANUSA-East, USDA
Forest Service, Northeastern Forest
Experiment Station, 370 Reed Road,
Broomall, PA 19008

My purpose is to provide background information on the spruce budworms and point out some insect-host interaction relationships that have been noted by others. These and other interactions will be discussed in more detail in the papers that follow.

There are several budworms that feed on forest trees. For our discussions, we will be interested only in the spruce budworm (Choristoneura fumiferana Clemens) and the western spruce budworm (C. occidentalis Freeman). Other budworms that may be referred to are the 2-year budworm (C. biennis Freeman), jack pine budworm (C. pinus Freeman) and Modoc budworm (C. viridis Freeman). These are all native insects of coniferous forests in North America.

The spruce budworm and western spruce budworm are responsible for significant defoliation in North America. For example in 1982, nearly 24 million hectares or 60 million acres of fir and spruce were visibly defoliated by these insects. There was significant tree mortality at all locations, especially in the East.

I shall briefly review the life history of both budworms to provide a common ground.

Until recently, these species and several near relatives were considered to be strains of C. fumiferana. As a result, much early information concerning the western species was published under the name of the spruce budworm. These two budworms have similar life cycles and habits, but differ in geographic range and hosts. I'll use the spruce budworm as an example and note any differences for the western spruce budworm.

Life Cycle and Habits

The spruce budworm has a 1-year life cycle. The rate of development of each stage depends upon climatic factors that vary with geographic regions; thus the following calendar times are only approximate. In the Northeastern United States and Canada, moths lay their eggs in July. In the West, eggs are laid in July and August. Female budworms lay about 150 eggs in masses of about 20 eggs per mass. Ocasionally, egg masses with up to 60 eggs are found. The eggs are light green and are laid in shingle-like fashion, generally on the undersides of needles. Occasionally they appear on the top surface of the needle or overlapping upper and lower surfaces, and at times even on the bark. Egg masses are generally most abundant on shoots in the outer perimeter of the tree crown.

The eggs hatch in about 10 days to 2 weeks. Budworm larvae require six developmental stages or instars from hatching to pupation. Hatching and emergence of first-instar caterpillars are usually complete by mid-August, when one of the two major dispersal periods occurs. Small larvae react photo-positively to light and move upward toward the branch tips. During this activity, some larvae may spin down on silken threads and be carried away by air currents. Such movement or dispersion spreads the larvae over a wide area, but also results in the death of many larvae. Budworm larvae remaining on host foliage do not feed but instead spin cocoon-like shelters (hibernacula) within which they soon molt to the second instar. The budworms overwinter in this stage, preferably on old flower scars on bark scales, or where lichen grows on branches.

In April or May of the following year, second-instar budworms emerge from their hibernacula. Again in response to light, the larvae move toward the branch tips, and the second major airborne redistribution occurs. Again, some larvae drop on silken threads and are blown about by air currents. When these larvae land on suitable host foliage, they begin to feed. Larvae become established in needles of 1-year-old foliage or mine directly into the expanding vegetative buds. Larvae will preferentially eat the more nutritious staminate flowers of balsam fir (Abies balsamea (L.) Mill.), when available. Typically, only one balsam fir needle is mined by each larva and the larva molts to the third instar either within the confines of the needle mine or soon after it leaves the needle. By late May or early June, third-instar budworms begin feeding on the newly opened vegetative buds. Larvae feeding on staminate flowers remain in place until the food supply is exhausted; then they move to the new, expanding foliage.

Late-instar (L_4-L_6) budworms are found from early June to early July. A full-grown sixth instar ranges from 0.75 to 1 inch (2 to 2.5 cm) in length. The body is dark brown with yellowish spots along the back. The head capsule and collar are dark brown or black. The sixth-instar budworm consumes a greater percentage of foliage than any other instar. At sparse population levels, larvae feed only on young needles of current shoots. Sixth-instar budworms normally web two or more shoots together, forming a feeding shelter. When populations reach outbreak levels and all new foliage is consumed, the larvae are forced to feed on old foliage. This phenomenon, called back-feeding, can result in noticeably smaller pupae and smaller egg masses, presumedly because older foliage is less nutritious. As foliage is depleted, larval movement increases, and many larvae drop from the defoliated trees to feed on understory host seedlings and young trees.

Pupation occurs within the feeding shelters or other protected locations. A newly formed pupa ranges from 0.5 to 0.75 inches (1.3 to 2 cm) in length and is green when first formed, but becomes yellow. With age the pupa darkens to a dark gray or dark brown. In the East, pupation occurs in late June and lasts from 8 to 12 days. Elevation and aspect, of course, affect these times in the West. In the West, pupae may be found from mid-July to early August.

Moths are present in the field from late June to mid-August. The spruce budworm is usually grayish with dark brown markings and has a wing span of about 0.75 inches (2.0 cm). Color pattern varies: some moths have a more brownish or reddish tinge with the gray markings. The western budworm is slightly larger and has a conspicuous white dot on the outer margin of each forewing. Adults live about 2 weeks, during which time they do not eat. The male locates the female for mating when she releases a sex pheromone. Once mated, females generally do not fly until they have laid at least part of their egg complement. After laying most of their eggs, though, females are active fliers. Given proper weather conditions, both male and female moths may be transported great distances by winds and storm fronts. Such long-range dispersal affects population trends and brings the budworm to new areas.

Hosts

The spruce budworm inhabits the northern coniferous forest of the eastern half of North America. Larvae feed on a number of conifers, but balsam fir, white spruce (*Picea glauca* (Moench) (Voss), and red spruce (*P. rubens* Sarg.) are the major hosts in eastern North America. Black spruce (*P. mariana* (Mill.) (B.S.P.) is occasionally attacked, as are eastern hemlock (*Tsuga canadensis* (L.) Carr.), tamarack (*Larix laricina* (Du Roi) K. Koch), and white pine (*Pinus strobus* L.).

The forest types of eastern North America differ from west to east. In the Lake States region, balsam fir, white spruce, and black spruce are the major sources of food. These conifers occur in patches that average 15 to 25 acres (6 to 10 ha) and are separated by hardwood or mixed-wood stands. Where hemlock is a common associate, it can be defoliated and more easily killed. In Maine and the Canadian Maritime Provinces, the patchy pattern gives way to extensive areas of softwoods. In this region red spruce becomes a major component of the forest, replacing the white spruce component.

The western spruce budworm is isolated from its eastern sibling species by the mid western prairie that divides the continent. The western spruce budworm causes the greatest economic damage in stands of Douglas-fir (*Pseudotsuga Menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Doug. ex D. Don) (Linde), white fir (*A. concolor* (Gord. & Glend.) Lendl. ex Hildebr.), subalpine fir (*A. lasiocarpa* (Hook.) Nutt., blue spruce (*Picea pungens* Engelm.), Engleman spruce (*P. englemanni* Parry ex Engelm.) and white spruce (*P. glauca* (Moench) Voss.) Occasional hosts are corkbark fir (*A. lasiocarpa* var *arizonica* (Merriam) Lemm.), Pacific silver fir (*A. amabilis* Dougl. ex Forbes), Western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contonta* var. *latifolia* Engelm.), ponderosa pine (*P. ponderosa* Dougl. ex Laws.), and western white pine (*P. monticola* Dougl. ex D. Don).

Balsam fir is the most vulnerable host, followed in order by white spruce, red spruce, and black spruce. It takes several years of defoliation to kill a tree. Fir will die after 4 to 7 years of repeated severe defoliations. White and red spruce can withstand at least an additional year or two of complete defoliation before dying. Generally, black spruce is not killed by budworm feeding except in the most severe outbreaks.

Severe defoliation by both budworms results in decreased tree growth, tree deformity, top killing, and finally death of trees, often over extensive areas. In fact, feeding habits can vary with the tree host and region. Both budworms may begin to feed on staminate flowers and conlets and complete their development on new foliage. In the northern Rocky Mountains, large larvae often feed on cones and seeds of western larch and Douglas-fir, then pupate in the cones.

Host-Insect Interactions

The relationship between the insect and its host tree is mediated by a number of physical and chemical factors. Some of these function in an all-or-none fashion, and their presence, even in small quantities, can render the plant completely unacceptable to some insects while having little effect on others. This so-called qualitative type of defense is exemplified by toxins such as alkaloids, terpenes and cyanide. Other factors function in a more quantitative manner and the degree of host suitability is inversely proportional to the level of the defensive factor in the host. Tannins, terpenes, and foliage toughness are examples of quantitative defenses. The distinction between these two classes of plant defense is arbitrary and not absolute. A given factor can function as a toxin to one insect and a quantitative defense to another. Generally, factors that make certain tree species immune from attack are likely qualitative, whereas factors that influence the susceptibility of a given tree species under different conditions, such as on different soil types, are likely quantitative. A close examination of the various interactions between the budworms and their primary hosts may provide important clues about the processes that make trees susceptible or resistant to damage by defoliation. Various characteristics of the tree or insect can be used to measure or quantify these interrelationships. Many of our speakers will be talking about such tree or insect characteristics as: growth rate, either radial or terminal, or development rate of the insect stages; phenology of tree development--whether it be synchronous or asynchronous with the insect; organic and inorganic compounds within the tree and their influence on the insect; available moisture for the tree and insect; fecundity of the insect; specialized sensors or organs in the insect for detecting special information in the environment or to cope with toxic plant substances. This latter category is relatively new and is just beginning to receive special attention.

The combination of these tree or insect characteristics has evolved into a complex system for the coexistence of the tree and insect. An examination of the historical record of the spruce-fir forest and recorded outbreaks of the spruce budworms reveals that when this complex biological system is left alone, both tree and insect species continue to exist in spite of vast mortality in populations of each. However, our perceived economic needs will not permit this natural progression.

Budworm outbreaks generally begin when there is an abundant supply of food; population crashes, on the other hand, usually occur only when the food supply is depleted. Various observations and studies have demonstrated that 3 to 4 years of severe defoliation result in a small complement of foliage with a suspected reduction in foliage quality, and therefore correspondingly smaller insects. These insects seem to function normally but their fecundity is clearly reduced (Miller 1963).

Variation in foliar nutrient content has been reported for various host species over time and by location (Shaw and Little 1972, Czapowskyj 1979). This variability is believed to play some role in the population dynamics of the budworm (Miller 1963). At least one research report has been able to provide evidence of a connection between foliage quality and insect development. Shaw, et al. (1978) were able to show that the addition of fertilizer to young balsam fir resulted in larger spruce budworms and higher survival. But attempts to demonstrate a relationship between insect survival or mature insect size and natural variations in foliar components have not been successful (Harvey 1981).

At the inception of a spruce budworm outbreak, a frequent observation is that individual host trees react differently to defoliation. This suggests that there are some differences in susceptibility (McDonald 1981). Unfortunately, as the budworm population increases these differences seem to disappear. This early evidence seems to suggest that a long-term program to develop resistant trees for planting would not be effective. However, these data are not vigorous or substantial. Hence, there still is reasonable expectation of finding and developing less susceptible cultivars of fir and spruce.

All primary host trees seem to be acceptable food sources, although there are some substantial differences between them in their capacity to grow budworms. Intuitive evidence seems to imply that foliage quality has some subtle influence on the population dynamics of the spruce budworms. Foliage quality differences likely provide some type of fine tuning or feedback information to this complex forest-insect system that might, for instance, induce budworms to disperse.

I believe the participants at this workshop will present research results to show that there are some quantifiable relationships between foliage quality and the budworms' population dynamics. Up to this point, work on foliage quality appears to have been conducted independently by entomologists and physiologists. The participants in this workshop represent these disciplines plus genetics, chemistry, forestry, and modeling. Some people believe that the best way to develop an understanding of the workings of host-insect interactions is through an interdisciplinary team approach. I hope this workshop will at least foster useful dialogue between these disciplines.

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GYPSY MOTH HOST INTERACTIONS: A CONCEPT OF ROOM AND BOARD

William E. Wallner

USDA Forest Service, Northeastern Forest Experiment
Station, Center for Biological Control of
Northeastern Forest Insects and Diseases, 51 Mill
Pond Road, Hamden, CT 06514

The influence of host type and condition on the bioecology of gypsy moth are discussed from the viewpoint of room and board. Larval establishment was higher on preferred hosts; less than 5% migrated off them. Nonpreferred hosts lost 10-25% of larvae. Susceptibility of gypsy moth larvae to nucleopolyhedrosis virus increased following 1 or 2 years of defoliation. Survival value of insect resting locations on the host tree and in the litter are discussed in connection with risk of predation.

> "And what does it live on?"
> "Weak tea with cream in it."
> "Supposing it couldn't find any?" she
> suggested
> "Then it would die, of course."
> "But that must happen very often,"
> Alice remarked thoughtfully.
> "It always happens," said the Gnat.
>
> Lewis Carroll, Through the Looking Glass

When attempting to describe the bioecology of gypsy moth, one cannot dissociate this ubiquitous insect from its host(s). While one tends to relate host-insect interactions to herbivory (board), other functions of the host (room) are inextricably linked with behavior and survival of the gypsy moth.

Fully embryonated eggs overwinter in masses containing from 250 to 1,000 eggs. Eclosion occurs from mid-April to early May, depending upon geographic location and spring weather, usually in synchrony with host budbreak; asynchrony may occur, however, in previously defoliated hosts, which tend to break bud later than normal. Most eggs in a mass hatch within 3 to 5 days; masses on a site may hatch over a period of 2 to 3 weeks, depending upon their location in the stand and exposure to solar radiation. First-stage larvae may remain on the mass for several days if conditions are unfavorable (rain, temperatures <40°F). Otherwise, they move to the top of trees in response to light, initiate feeding or suspend themselves on silk, which fractures, permitting the larvae to disperse over several hundred meters (Mason and McManus 1981). Redispersal undoubtedly occurs and although the events that trigger it are unknown, it is believed to be related to the vigor of the larvae and means of host selection (Capinera and Barbosa 1976). Gypsy moths feed on more than 300 species of trees and shrubs and these have been grouped loosely into preferred, intermediate, and nonpreferred or rejected species (Bess et al. 1947, Houston 1979). Species of oak rank among the most preferred.

Once settled, first-stage larvae confine their feeding to the inner perimeter of the upper leaf surface. Second-stage larvae feed in inner leaf perimeter holes, whereas third-stage larvae feed on holes but expand their feeding activity to leaf margins. Larvae remain in the canopy; first-stage larvae rest on the lower leaf surface and second- and third-stage larvae rest on the undersides of twigs, branches, or bole; fourth- to sixth-stage larvae feed on the leaf margins (Leonard 1970). Normally, males have five instars, females six. Feeding activity is concentrated in the outer and upper crown and proceeds downward as foliage is removed by browsing. Dramatic behavioral change accompanies molting to the fourth stage; larvae feed nocturnally and migrate down to resting locations. Where defoliating populations are dense, larvae remain in the canopy, have intermittent feeding bouts day and night, and refrain from migrating to resting locations. This change in behavioral and feeding strategy is not understood, but it may be related to effects of crowding, necessity to maintain moisture balance, or abandonment of resting locations whose integrity has been destroyed by increased radiation due to defoliation.

Defoliation is usually a 1- to 2-year phenomenon, with outbreaks being terminated abruptly by starvation, desiccation, virosis, or a combination of factors. Forest stands on moist sites that are repeatedly defoliated tend to become more resistant to defoliation. This stems from the fact that preferred tree species, which are consistently defoliated more heavily, are more likely to die (Campbell and Sloan 1977).

Is gypsy moth capricious? If so, does larval behavior reflect this penchant? Host type influences rates of development, survival, and fecundity (Hough and Pimentel 1978) but larval distribution and movement within a forest stand are poorly understood.

In 1980, I selected a mixed hardwood stand classified as susceptible to gypsy moth defoliation, and determined that there were 22 egg masses within a 1/2-ha study area (considered a sparse population). All trees >3 inches DBH were burlap-banded and larvae marked under bands every other day with a different color acrylic paint for each of eight tree species. The assumption was made that each tree had an equal chance of receiving dispersing or redispersing larvae, and that host selection was made by instar I and II larvae. Larval abundance was related to gypsy moth host preference; the greatest numbers of larvae/ft^2 of basal area of host were found on oak, hickory, and aspen; the fewest on red maple, dogwood, and black birch (Table 1). Once larvae reached the third stage, they usually remained on the same host. Less than 5% of the larvae left preferred hosts. Some redistribution is expected since larvae can be dislodged from foliage to the ground by wind, rain, parasites, or predators. They then head for the nearest vertical object and climb it. Least preferred hosts lost more instar III larvae than preferred hosts, which lost none. Additionally, 10 to 25% larval outflux of instars V and VI occurred on least preferred hosts (Table 2). Redistribution appeared random but certain preferred hosts (aspen)

Table 1.--Number of gypsy moth larvae captured and egg masses counted/ft.^{2} basal area of host. North Stonington, CT, 1980

Instar	Quaking aspen	Black oak	White oak	Hickory	Black birch	Red maple	Dogwood
III	2.5	5.0	2.3	7.9	3.7	1.9	0.4
IV	32.4	14.3	12.7	26.1	16.7	12.2	2.6
V	118.7	43.1	41.0	60.6	58.6	36.6	14.8
VI	82.2	33.1	38.3	37.0	48.5	17.9	9.9
# Egg masses	48.1	27.7	53.6	21.8	30.4	11.3	1.4

Table 2.--Percent marked gypsy moth larval movement/ft.^{2} basal area by instar and host. North Stonington, CT, 1980

Instar	Quaking aspen	Black oak	White oak	Hickory	Black birch	Red maple	Dogwood
			Percent larval outflux				
III	0	0	0	0	3.9	7.7	0
IV	3.6	2.0	4.6	1.7	5.2	4.7	1.9
V	3.3	3.0	3.2	4.3	10.1	14.6	7.8
VI	5.6	3.5	2.3	3.5	2.7	25.8	4.8
			Percent larval influx				
III	22.2	0.3	0	0.6	0	0	0
IV	6.0	2.3	2.5	1.2	2.5	3.2	11.5
V	5.6	3.8	4.9	3.0	10.2	6.3	7.4
VI	6.1	2.2	4.5	3.2	8.3	11.8	8.1

gained more marked larvae from other hosts than they lost. In general, there was little evidence of consistent host-switching on preferred or intermediate hosts.

Utilization of the burlap bands increased with each instar reflecting that larval migration down the tree is influenced by the size and abundance of resting locations. Burlap bands are considered highly attractive as resting locations, and egg mass abundance was correlated with the numbers of stage VI females. Only white oak had more egg masses than sixth instars. No evidence of preferential movement from other hosts to white oak was disclosed by our larval marking procedure. Perhaps white oak provided the ideal room and board through preferred foliage and abundant refuges above our burlap bands which precluded the need by all larvae to migrate down the bole where they could be marked.

Pupae are usually found in those resting locations used by larvae that offer the most protection from predators (Campbell et al. 1975). Although this symposium focuses largely on the tree as board for the herbivore, the host may provide room for gypsy moth by providing refuges more secure than others.

> The Traveller that is struck by
> Lightning, seldom gets home to
> Tell his widow.
>
> Ben Franklin's Wit & Wisdom

Analogously, predators can strike quickly and preferentially kill larvae or pupae. The tree provides a number of resting locations (room) each having an associated level of risk to the larva or pupa occupying it. Smith (in press) reported that the type of resting location influenced pupal mortality from predators. Pupae have higher survival when the host provides refuges off the ground that are more secure from predation (Table 3). Forest stands susceptible to gypsy moth defoliation can be classified on several factors including the abundance of these structural features (Houston and Valentine 1977).

The abundance of gypsy moth in Eurasia and East Asia is cyclic and predictable. In North America it is considered episodic, and outbreaks are unpredictable. The consistent level of nonpathogenic mortality reported by Campbell and Podgwaite (1971) in sparse to moderate densities gives credence to the notion that a general decrease in physiological dysfunction

Table 3.--Percent survival of gypsy moth pupae within different resting locations

Density per acre	Location	Eaten by predators		Died (other causes)	Emerged
		Vert.	Invert.		
1000	Flap	13	19	15	52
	Bole	14	17	17	52
	Litter	45	22	8	25
300	Flap	7	15	11	68
	Bole	22	19	11	49
	Litter	42	25	7	26
100	Flap	2	13	6	78
	Bole	3	14	8	76
	Litter	9	37	3	52

From Smith, 1983

among larvae could signal the initiation of an outbreak. A number of authors have speculated on host foliar condition relative to the abundance of other tree defoliators; nitrogen (White 1974), tannins (Feeny 1970, Schultz and Baldwin 1982), and wound-induced proteinase inhibitors (Green and Ryan 1972). Gypsy moths reared on trees that had been artificially defoliated to simulate insect defoliation took longer to develop, suffered more nonpathogenic mortality, and developed into smaller pupae than those on undefoliated hosts (Wallner and Walton 1979). Foliar analysis for nutritional changes which occurred in conjunction with this study (Valentine et al. 1983) indicates that foliar sugar concentration may influence gypsy moth growth and fecundity.

There are subtle secondary effects that are scientifically appealing but elusive to document. One, increased susceptibility to a pathogen as a consequence of declining host constituency, was examined in the course of our study on the effect of artificial herbivory on gypsy moth. Larvae were constrained on host trees receiving 1, 2, or no defoliations and permitted to develop to adults, from which eggs were obtained by within-treatment matings. Larvae from eggs from each of these 3 populations subjected to different defoliation regimens were challenged with the nucleopolyhedrosis virus (NPV) (Lewis et al. 1981) and LC_{50} values were determined (Fig. 1).

Only those larvae from eggs produced on trees defoliated for 2 consecutive years were significantly more susceptible to NPV than those from undefoliated trees. However, larvae from once-defoliated trees tended to be more susceptible to NPV than those from either the primary standard or undefoliated trees. This suggests that host condition can influence the resistance of the insect to a pathogen. NPV assays traditionally have been variable, depending upon the geographic source of gypsy moth, its past defoliation history, bioassay methodology, etc.; hence this one test should be viewed as only identifying a potential area for further research.

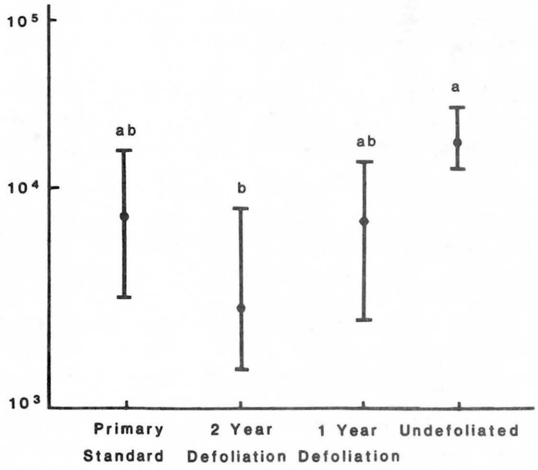

Figure 1--LC $_{50}$ and 95% confidence limits cf gypsy moth mortality challenged with 1976 K standard gypsy moth NPV. Larvae emanated from eggs produced by field reared insects on trees subjected to different defoliation treatments.

The host mediates gypsy moth development, behavior, physiology, and survival within the concept of room and board. It cannot be viewed as a static relationship but a dynamic one, a theme which should be evident throughout this workshop. Are gypsy moth and spruce budworm host relationships iterative processes such that--

> The food that to him is as lucious
> as locusts, shall be to him shortly
> as bitter as coloquintida.
>
> William Shakespeare, Othello

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SELECTION FOR INSECT RESISTANCE IN FOREST TREES

Donald H. DeHayes

School of Natural Resources, Department of Forestry, The University of Vermont, Burlington, VT 05405

An interdisciplinary approach to resistance breeding is discussed with emphasis placed on documenting genetic variation and developing an understanding of the causal mechanisms responsible for variation in host susceptibility. The specific features and effectiveness of phenotypic and genetic selection are contrasted and examples of documented genetic variation in susceptibility of trees to insects are provided.

Introduction

Despite progress in controlling insects through chemical application and biological manipulation, economic losses from insect damage to forest and ornamental trees remain enormous. Although genetic methods have proved successful in development of insect-resistant crop plants (Maxwell and Jennings 1980), progress in breeding insect resistant trees has lagged behind. As pointed out by Hanover (1980), that lag can be attributed, at least in part, to relatively long generation intervals in trees and a dearth of knowledge about host physiology and insect biology. In addition, the development of resistance in a long rotation host such as trees requires an interdisciplinary research effort which has only rarely been put forth. The objective of this paper is to discuss the major components and implications of resistance breeding strategies for trees rather than to provide a review of resistance concepts or physiological mechanisms involved in resistance. The latter information with respect to trees is addressed in reviews by Stark (1965), Gerhold et al. (1966), Hanover (1975 and 1980). Hopefully this paper will contribute to the stimulation of interdisciplinary discussions and perhaps cooperative research endeavors among geneticists, physiologists, and entomologists from the northeast.

Components of Resistance Breeding

In the simplest sense, one can identify two major components of the resistance breeding strategy for trees. The existence and accurate demonstration of host variation in resistance (or susceptibility) to insect attack is prerequisite to selection or breeding for insect resistance. Secondly, a thorough understanding of the nature and underlying mechanism(s) responsible for the observed variation in resistance is important to determine the feasibility and directions of future breeding efforts. A third component, the actual breeding of resistant strains, is dependent upon the success of the first two components. In my estimation slow progress toward developing resistant strains of trees (or, at least, strains with reduced susceptibility) can be attributed to the lack of a concerted interdisciplinary effort in the documentation and understanding of insect resistance and its mechanisms. For instance, genetic improvement programs have been established for balsam fir in the Lake States and New England, but none of the many provenance and progeny test plantations have been placed within major spruce budworm regions. As a result, the most productive method for revealing variation in insect susceptibility has not been utilized and no progress has been made in the development of balsam fir resistant to the budworm. With respect to the second component, numerous examples exist of physiologists and biochemists who have thoroughly studied the morphology, anatomy, and/or chemistry of tree populations with purported but not documented resistance to an insect pest. In contrast, enough information on the actual breeding of resistant strains has been generated from crop research (Painter 1966) to provide an adequate foundation of breeding information once the first two components are successfully investigated for a particular host-insect system.

Variation in Host Susceptibility

The development of host resistance to insect attack must be preceded by at least some level of heritable variation in susceptibility to an insect pest. Such genetic variation may occur naturally within species and may be represented by variation among races, provenances, families or individual trees growing side by side in the same stand. In the absence of natural intraspecific variation in susceptibility, interspecific variation may exist and species selection may be a reasonable means of circumventing economic losses resulting from insect attack (Wright and Gabriel 1959; Wilkinson 1981). If species selection is not appropriate, then species hybridization may be an expedient way to generate sufficient heritable variation to allow selection to be productive.

When considering the distribution and biology of the host, the potential for variation in susceptibility of trees to insect attack is expected to be quite high. For instance, tree species have large natural ranges and are, therefore, subjected to a diversity of climatic, edaphic, and biological pressures which tend to promote genetic variation, at least at the population or regional level. Rangewide provenance tests of many species have revealed considerable genetic variation in morphological, anatomical, biochemical, and physiological characteristics, and would suggest that the potential for variation in insect susceptibility might also be high. In addition, despite the increase in tree cultivation during recent years, the vast majority of the forest resource exists in extensive, relatively wild stands. As a result, there probably has not been much gene depletion or a drastic narrowing of the genetic base for most species. Furthermore, tree species are largely outcrossing organisms and are considered to be highly heterozygous with respect to most traits. High heterozygosity can be expected to lead to considerable genetic diversity among individual trees as well as at population and racial levels. Finally, a substantial level of interspecific compatibility seems to exist within many genera of forest trees and numerous hybrids among species have been produced and documented. Therefore, even in cases where natural variation within a tree species is quite low, the possibility of creating new variation through species hybridization is possible and plausible.

Mechanisms Responsible for Variation in Susceptibility

Upon identifying variation in host susceptibility, it is important to confirm a genetic component to that variation and to understand the underlying causal mechanism(s) responsible for the observed variation. It is important, for instance, to understand whether variation in susceptibility is due to some genetically-controlled avoidance factor (eg. phenological asynchrony) or whether the host is actually capable of resisting the insect. Although resistance can theoretically be identified, and perhaps even captured through breeding, without an understanding of causal mechanisms, the efficiency of breeding and stability of resistance will increase considerably with knowledge of the chemical, physical and/or physiological basis for resistance. This is especially true for long rotation crops such as trees. Instead of "blindly" breeding for resistance, one can select directly for the character(s) which confer that resistance. Or, as emphasized by Hanover (1980), study of causal mechanisms could facilitate indirect selection for traits with a strong genetic correlation with resistance but not causally related to it. Furthermore, physiological investigations of resistance mechanisms may reveal host chemicals which can be used as insecticides or as vehicles of insect behavior modification (Hanover 1980).

Studies addressing mechanisms of tree resistance often examine specific biological properties of the host (and perhaps the insect) and attempt to relate variation in such characterisitcs to variation in susceptibility to an insect pest. Hanover (1976) has discussed tree resistance to insects in terms of variation in the following broad categories of host characterisits: morphology and anatomy of the host, chemical repellants produced by the host, chemical attractants produced by the host, and the nutritional status of the host. In my opinion, research into mechanisms of insect resistance is necessary for the development of an effective resistance breeding program, but is complicated by environmental influences, tree responses to injury, and developmental, seasonal, and within-tree variation.

Selection for Resistance

Before physiological or chemical mechanisms of resistance can be described and natural variation in insect resistance can be exploited toward the development of resistant strains, it is essential that individual trees or tree populations with inherently low susceptibility to insect attack be accurately identified. This involves some form of selection. Since "selected" trees will be the source of investigations of resistance mechanisms and may form the basis of a resistance breeding program, it is mandatory that resistance of these trees is documented rather than assumed or inferred. Although often taken for granted, the chore of selection for resistance is difficult because of the quantitative and complex nature of the host-insect relationship, environmental influences on this relationship, and interactions between host and insect genotypes and the environment. The major approaches to selection are phenotypic selection of resistant trees in natural or planted stands and genetic selection of families or provenances from replicated progeny tests.

Phenotypic selection

If no previous information on genetic variation in resistance is available for a given host-insect situation, phenotypic selection of unattacked or completely recovered individuals in heavily infested stands is a logical initial step in an artificial regeneration program designed to improve insect resistance. Obviously, in such situations, one hopes that the apparent resistance or recovery ability of the parent tree is inherited and can be transmitted through seed or vegetative propagules to the offspring. For phenotypic selection to be effective, a high selection differential should be maintained (i.e., many trees should be observed but only the one or two best should be selected in each stand) and factors that could lead to escape or an apparent resistant condition must be considered in the assessment of candidate trees (McDonald 1981). However, since the genetic component of phenotypic variation is not readily ascertained without replicated progeny tests, there can be no assurance that progeny will exhibit increased resistance. In fact, there can be no assurance that the selected parent tree has exhibited true resistance. Although phenotypic selection is a reasonable improvement approach when no other information or alternatives are available, it is not the most efficient approach toward initiating a research program involving phyisological investigations into resistance mechanisms and actual resistance breeding. Clearly, the rigorous demonstration and documentation of genetic resistance to insect attack should be prerequisite to physiological investigations and advanced breeding efforts. Such documentation can not be attained with phenotypic selection in the absence of progeny tests. Unfortunately, the vast majority of research addressing the physiology and genetics of insect resistance in trees has been conducted in the absence of documented genetic resistance of the host.

Specific features of phenotypic selection which limit its utility in screening for and understanding the nature of insect resistance are as follows:

1. Selection procedures. The effectiveness of phenotypic selection is influenced largely by the selection differential employed and the specific methods utilized in selecting can-

didate trees as well as the heritability of the trait in question. Although it may be possible to standardize selection methods, the selection differential may vary with the size, age, and degree of infestation in the stands.

2. Escape rather than resistance. Unless a reliable repeatibility estimate can be included in the selection criterion, the possibility exists a candidate has escaped rather than resisted attack. Although the probability of escape is inversely proportional to the degree of infestation in the stand, it can theoretically never be zero.

3. Microsite effects on host and insect phenotype. Localized climatic, soil, or biological factors can influence the morphology, chemistry, and phenology of the host, insect, and/or insect predators and perhaps create a temporarily induced resistance (pseudoresistence). Such confounding environmental factors also muddle interpretation of physiological parameters measured on phenotypically-selected trees.

4. Developmental and age variation of host. Individual trees may not be attacked because of developmental factors associated with age rather than genetically controlled physiological factors.

5. Narrow genetic base. Since phenotypic selection is often concentrated in a relatively small portion of a species range, only a small portion of the speices genome is assessed. This narrow genetic base limits the potential for developing resistant strains and could lead to some level of inbreeding depression in advanced generation populations.

6. Nature of genetic control. Even if escape, microsite factors and age can be eliminated as confounding variables and genetic resistance is strongly suspected, the transmissability of resistance through seed is dependant on the nature of genetic control. If resistance of an individual is the result of a specific combination of non-additive genes, one can not expect a consistently high level of resistance in offspring of that parent.

7. Stability of resistance. Since for an individual tree there is no way to test the repeatibility of resistance over space, it is not known whether the apparent resistance is stable over different environments or is the result of a specific genotype x environment interaction.

8. Cost and logistics. The cost of maintaining a high selection differential and broad genetic base in a phenotypic selection program can be prohibitive. Furthermore, the logistics of field measurements of physiological traits and of actual breeding are made complicated by tree size, and travel distances as well as confounding environmental factors.

Phenotypic variation in insect susceptibility has been observed for many forest tree species, but only rarely has there been documentation of genetic variation or a physiological explanation for the apparent resistance. For instance, based on phenotypic observations, Hall (1937) reported that "Shipmast" and "Higbee" cultivars of black locust were resistant to the locust borer, but the apparent resistance "broke down" following additional testing. In balsam fir, phenotypic variation in susceptibility to black-headed budworm and spruce budworm has been reported but genetic resistance has never been substantiated (Bakuzis and Hansen 1966). Numerous attempts have been made at phenotypically selecting eastern white pines that are resistant to the white-pine weevil. For instance, Wright and Gabriel (1959) used sophisticated probability estimates and adjustments for microenvironmental factors in assessing weevil resistance but were unable to reliably select resistant trees. In fact, despite phenotypic variation in susceptibility, recent research has indicated that there is no natural resistance of eastern white pine to the white-pine weevil (Wilkinson, personal communication). Finally, in a review paper, Hanover (1980) noted that the American bark beetles and their tree hosts have received more research emphasis than any tree-insect system in the world. Although apparent resistance has been observed in natural populations and considerable research has been done on possible resistance mechanisms, there has been no documentation of genetic resistance to bark beetles among their primary hosts, the pines, spruces, and Douglas-fir (Hanover 1980). Although phenotypic selection has been the foundation of most plant breeding programs, its limitations and expenses with respect to selection of insect resistant trees must be recognized. Wright and Gabriel (1959) provide a realistic account of the effort involved in selecting and testing apparently resistant phenotypes and McDonald (1981) has provided an excellent illustration of the potential complexity of a host-insect system and the numerous factors which could lead to phenotypic variation in response of a host to insect attack.

Genetic Selection

The most productive means for determining the magnitude and nature of intraspecific variation in insect resistance has been carefully designed progeny tests which are replicated within plantations and by several plantations at different locations. Such experiments include rangewide or localized provenance tests, half-sib and full-sib progeny tests and interspecific hybridization studies. These tests may examine progeny of phenotypically selected or unselected parents. In many cases, genetic plantations have been established with tree improvement objectives other than insect resistance in mind. However, if properly designed, such studies can be conveniently and accurately used to assess genetic variation in incidence of attack, degree of injury, feeding and oviposition preferences as well as physiological or biochemical characteristics which may be directly or indirectly related to host susceptibility. Some examples of documented genetic variation in susceptibility of tree species to insects are included in Table 1.

Some features of progeny tests which contribute to their value in assessing genetic variation in insect susceptibility are as follows:

1. Partitioning of variation. Variation in insect susceptibility and other traits of interest can be quantitatively partitioned into genetic, environmental, and genetic x environment components. As a result, the heritability of specific traits, stability of resistance, and expected gain from selection and breeding can be assessed. Also, genetic variation can be confirmed before expensive and time-consuming studies of resistance mechanisms are initiated.

2. Distribution of genetic variation. The distribution of genetic variation among races, regions, populations, families, and individual trees can be accurately estimated. Such information can help elucidate the nature of variation, such as adaptive strategies, as well as influence subsequent selection and breeding strategies.

3. Broad genetic base. Because trees grown from seed collected throughout a species range can be incorporated into a single study, a relatively broad portion of the species genome can be assessed. As a result, the probability of discovering genetic resistance is increased and the potential for maintaining a broad breeding population is enhanced.

4. Related traits can be accurately measured. Genetic variation in morphological, anatomical, physiological, and biochemical characteristics that may be related to insect susceptibility can be accurately assessed because the measurement of several trees per population or family provides a repeatability estimate.

5. Indirect selection. Genetic correlations among traits can be calculated so the effectiveness of indirect selection for resistance can be tested.

6. Developmental variation. Repeated assessments of variation in insect susceptibility provide an assessment of developmental and age x genetic variation. Juvenile-mature correlations can be estimated and used in judging the reliability of selections.

Table 1. Examples of documented natural genetic variation in susceptibility of tree species to insects.

Host	Insect	Reference
Scotch Pine	Pine Root Collar Weevil	Wright and Wilson, 1972
	European Pine Sawfly	Wright *et al*., 1967
	Eastern Pineshoot Borer	Steiner, 1974
	Zimmerman Pine Moth	Wright *et al*., 1976
	White-Pine Weevil	Wright *et al*., 1976
Eastern White Pine	White-Pine Weevil	Wright and Gabriel, 1959; Garrett, 1972
Austrian Pine	Zimmerman Pine Moth	Wheeler *et al*., 1976
Jack Pine	Eastern Pineshoot Borer	Jeffers, 1978
	White-Pine Weevil	Arend *et al*., 1961
	Red-Headed Pine Sawfly	Arend *et al*., 1961
	Northern Pitch Twig Moth	Hodson *et al*., 1982
Douglas-Fir	Sitka Spruce Gall Aphid	Teucher, 1955
	Douglas-fir Woolly Aphid	Meinartowicz and Szmidt, 1978
	Western Spruce Budworm	McDonald, 1979
White Spruce	Eastern Spruce Gall Aphid	Canavera and DiGennaro, 1979
Japanese Larch	Larch Sawfly	Harman and Genys, 1970
European Larch	Larch Sawfly	Genys and Harman, 1976
Norway Spruce	White-Pine Weevil	Holst, 1955
	Black-Marked Tussock Moth	Schönborn, 1966
Balsam Fir	Balsam Twig Aphid	DeHayes, 1981

7. Convenience for breeding work. Since all trees are gathered in one place and are all of the same age, breeding can be done with limited travel and usually on trees of relatively small size.

8. Immediate production of low susceptible populations. If a genetic component to variation in insect susceptibility is confirmed, open-pollinated seed can be collected from races, populations, or individual trees with low susceptibility and some level of resistance can be expected from the trees produced.

9. Phenotypic selection still possible. If genetic variation among populations or progenies is not evident, then phenotypic selection of individual trees can still be practiced in the even-aged test plantations in hopes of exploiting within-family genetic variation.

Although progeny tests are an excellent source of information concerning genetic resistance, they are only effective when located in insect prone areas and when they are of an age (or size) in which the trees are susceptible. For instance, progeny tests may not be an immediate source of information on genetic variation in susceptibility to most bark beetles, since these insects generally attack mature trees. Certainly, forest geneticists and entomologists can and should work cooperatively to insure that forest genetics test plantations are established in areas where insect populations are high so that differential susceptibility can be assessed some time in the future. Perhaps the most serious limitation to genetic selection for insect resistance through progeny tests, is that variation in susceptibility is assessed in unnatural plantations containing a diverse mixture of genotypes. It is possible that insects will select for or against certain seedlots when they are included in a mixed planting, but will attack indiscriminantly in commercial plantings containing trees from one or a few selected seedlots. Despite this potential difficulty, progeny tests still appear to be the only reliable means of documenting a genetic component to variation in susceptibility.

Much of the information documenting genetic variation in susceptibility of tree species to insect pests has been generated from observations of differential damage or feeding in rangewide provenance tests. Other tests, including species and hybrid trials as well as single-parent progeny tests, should also be monitored for such variation whenever possible. Many such tests already exist in the northeast and represent an as yet untapped source of potentially valuable information. Although documentation of genetic variation in susceptibility is an important initial step, studies defining the nature of the variation (eg. resistance vs. avoidance) and elucidating physiological causes for such variation need to be pursued. Cooperative research among geneticists, physiologists and entomologists will likely be the most expedient approach toward the development of forest trees that are resistant to insects.

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DOUGLAS-FIR PROGENY TESTING FOR RESISTANCE TO WESTERN SPRUCE BUDWORM

Geral I. McDonald

Principal Plant Pathologist, USDA Forest Service, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, 1221 S. Main Street, Moscow, ID 83843

Ample evidence exists that inland populations of Douglas-fir suffer varying amounts of defoliation by western spruce budworm (Johnson and Denton 1975; Williams 1967; McDonald 1981). Such variation in plant insect association can be the result of the plant escaping attack in time and place to actual confrontation between plant and insect (Harris 1980). Co-evolved genetic interaction between insect and plant is usually involved in initiation and preservation of plant polymorphisms, whether they be morphological or chemical responses (Gilbert 1982; Berenbaum 1983). Since western spruce budworm (Choristoneura occidentalis Freeman) is a native insect, there are three reasons for wanting to know more about the genetic nature of the Douglas-fir-budworm interaction. First, genetic interaction may hold the key to understanding budworm populations release and crash (Lorimer 1982). Second, a co-evolved and dynamically balanced genetic interaction may be keeping damage to levels biologically tolerable to Douglas-fir, which, if preserved, will provide the foundation for additional silvicultural and chemical controls (Browning 1980). The third reason is the possibility of actively breeding for unnatural levels of resistance for use in reforestation (Lamb and Aldwinckle 1980).

All investigations of genetics must begin with some observable difference in the target populations. Budworm feeding differences are readily apparent in western conifer populations (Williams 1967; McDonald 1981). These differences could be caused by factors ranging from asynchronous phenology (Manley and Fowler 1969) to a complex interaction of pheromones, mating, egg oviposition, and larval feeding preference (McDonald 1981). The first step to unlocking these secrets is progeny testing (McDonald 1982). Such tests have shown the presence of independent genetic components for larval feeding (family heritability = 0.43) and oviposition levels (stand differences) on 2-year-old Douglas-fir (McDonald, in press). One must conclude that some level of genetic interaction for one or both of these traits is functioning. More importantly, these traits may be reciprocally related to geographic variation of budworm populations as delineated by Willhite and Stock (1983) and discussed by McDonald (in press). Such geographic association could materially change seed and breeding zone requirements for inland Douglas-fir.

Since ecological adaptation has a genetic basis in Douglas-fir (Rehfeldt 1979), genotypes were expected to express consistent long-term growth patterns in response to their adapted environments. Patterns of radial stem growth were studied and found to be associated with a tree's ability to accommodate budworm outbreaks. The patterns of radial growth of dead or heavily defoliated Douglas-fir varied greatly, whereas paired, non-defoliated trees showed much more consistent growth patterns from year to year.

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A TECHNIQUE TO STUDY PHENOLOGICAL INTERACTIONS BETWEEN DOUGLAS-FIR BUDS AND EMERGING SECOND INSTAR WESTERN SPRUCE BUDWORM

Roy F. Shepherd

Canadian Forestry Service, Pacific Forest
Research Centre, 506 West Burnside Road,
Victoria, British Columbia, Canada
V8Z 1M5

A technique is described to relate seasonal development of buds of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, to larval emergence and survival of western spruce budworm (*Choristoneura occidentalis* Freeman) (Tortricidae). Losses of larvae due to asynchrony of emergence and bud swelling and the reduced protection of the bud following flush is illustrated.

Introduction

Host-insect synchronization is often important to the survival of the insect; for example, Witter and Waisanen (1978) found a six-fold difference in the mean proportion of buds infested by *Choristoneura* spp. between early and late flushing clones of *Populus tremuloides* Michaux. Information is lacking, however, on losses of western spruce budworm, *Choristoneura occidentalis* Freeman that occur because of poor synchronization of larvae emerging from diapause and the swelling of the buds of its host, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco.

Preliminary studies indicated that patterns of defoliation of Douglas-fir in mountainous situations could be related to weather during the bud mining period. In addition, usually there are trees in defoliated stands which escape severe injury (McDonald 1981) and the lack of synchronization between larval emergence and bud swelling may be the reason why these trees are able to retain their foliage. This paper describes the techniques developed to determine the variability of host-insect synchrony and how it affects insect survival and bud damage. An illustration is given of the type of information which can be obtained with this technique.

Methods

Five vegetative buds, 1 to 2 m from the ground, on each of 20 trees per plot were selected in early spring and tagged prior to bud swelling and larval emergence. Trees with a variety of heights were chosen; buds were selected from the upper crowns of trees 1 m high to the lower crowns of 30 m trees. Seven plots were selected to represent a range of weather patterns and budworm densities; bud and insect survival and development were followed on these plots. Buds were inspected weekly and estimates made of the following: number of newly mined needles, presence of larvae, bud developmental stage and type of bud damage. Mined needles were coded weekly, using typewriter correction fluid, as mined needles often dropped off within 2 to 3 weeks of attack. A 10X illuminating magnifier was used to detect larvae in developing buds without disturbing them. A hygrothermograph in a Stevenson screen was set up in a nearby stand opening to record temperature. Instars of larvae, collected weekly from adjacent non-study trees in each plot, were determined and correlated to degree days calculated using a 5° threshold.

Nine developmental stages of buds could be recognized and photoguides were used to aid in their identification (Fig. 1):

0 - Overwintering stage: uniform dark brown color, no swelling.

1 - White tip stage: bud beginning to swell, tip becoming sharp and light-colored.

2 - Yellow stage: at least 1/2 of bud yellow to light brown, individual scales not conspicuous.

3 - White scale stage: bud all light brown or yellow, scales separated to reveal white layers underneath.

4 - Columnar stage: bud columnar shape with a rounded tip, green needles visible beneath semi-transparent scales.

5 - Split stage: bud split open to reveal green needles, bud cap may still be present, needles still tight together.

6 - Brush stage: bud cap gone, needles flaring but little shoot growth so needles appear to arise from one location.

7 - Feather duster stage: shoot growth beginning and needle bases separating, needles not reflexed.

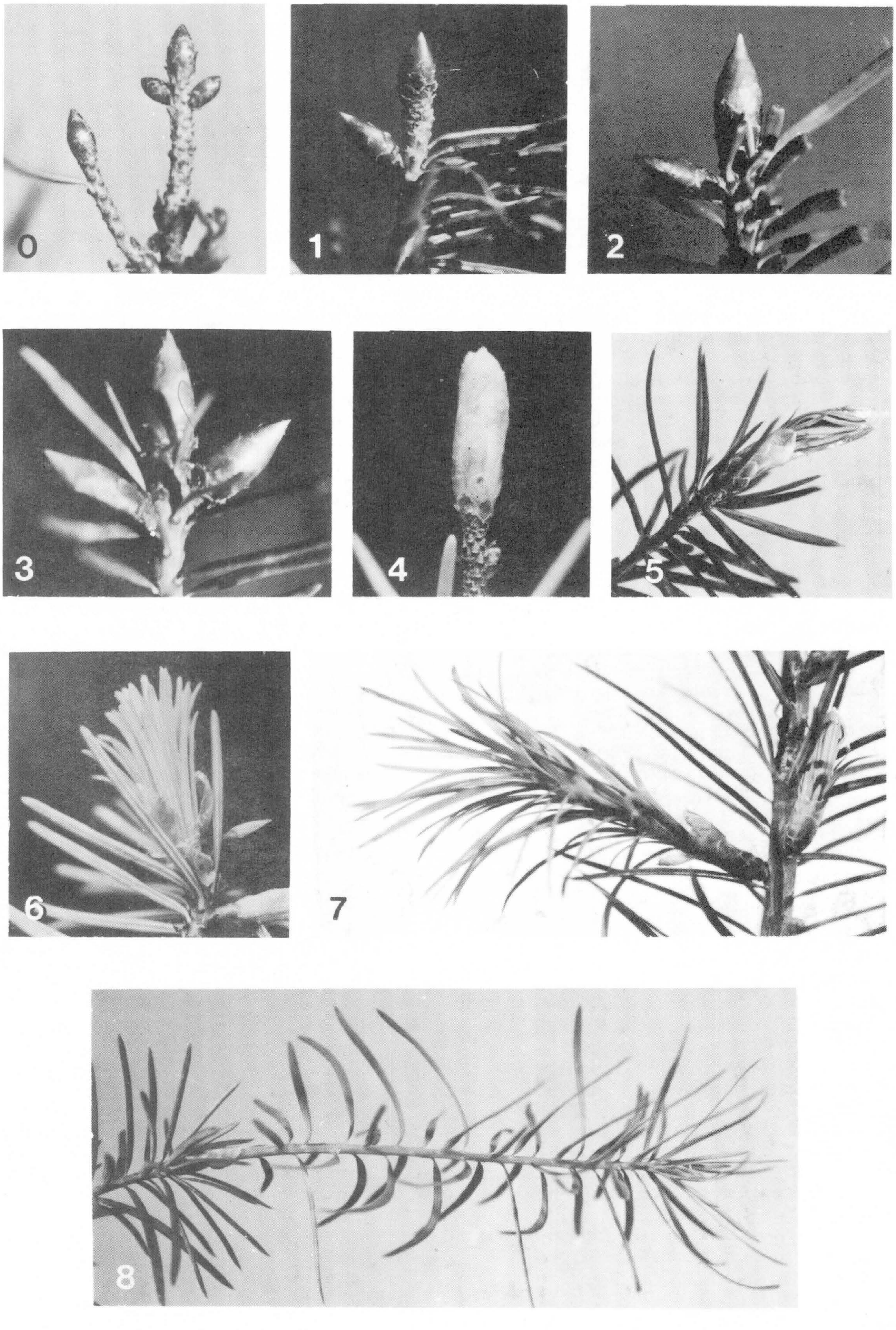

Figure 1. Photoguide of bud development stages 0 to 8.

8 - Shoot growth stage: needles reflexed and needle bases separated, new stem obvious.

These are similar to the six phenological stages recognized by Nienstaedt and King (1970) for Picea glauca (Moench) Voss and used by Pollard and Ying (1979) in studies of variability of flush rates.

Bud damage classes were noted as follows:

0 - bud or shoot not attacked.

1 - bud attacked and killed before it flushed.

2 - bud attacked, still alive, but has not flushed, extent of damage cannot be estimated.

3 - bud flushed and attacked, <75% of the needles have been damaged.

4 - bud flushed and attacked, >75% of the needles have been damaged, next year's bud healthy.

5 - bud flushed and attacked, >75% of the needles have been damaged, next year's bud killed.

Results

A time series graph can be constructed for each plot, one of which is illustrated in Figure 2. In this plot, larvae first began needle mining on May 6 and continued until May 31. By this date, half of the buds had swollen to stage 2 (Fig. 1), and the scales had thinned

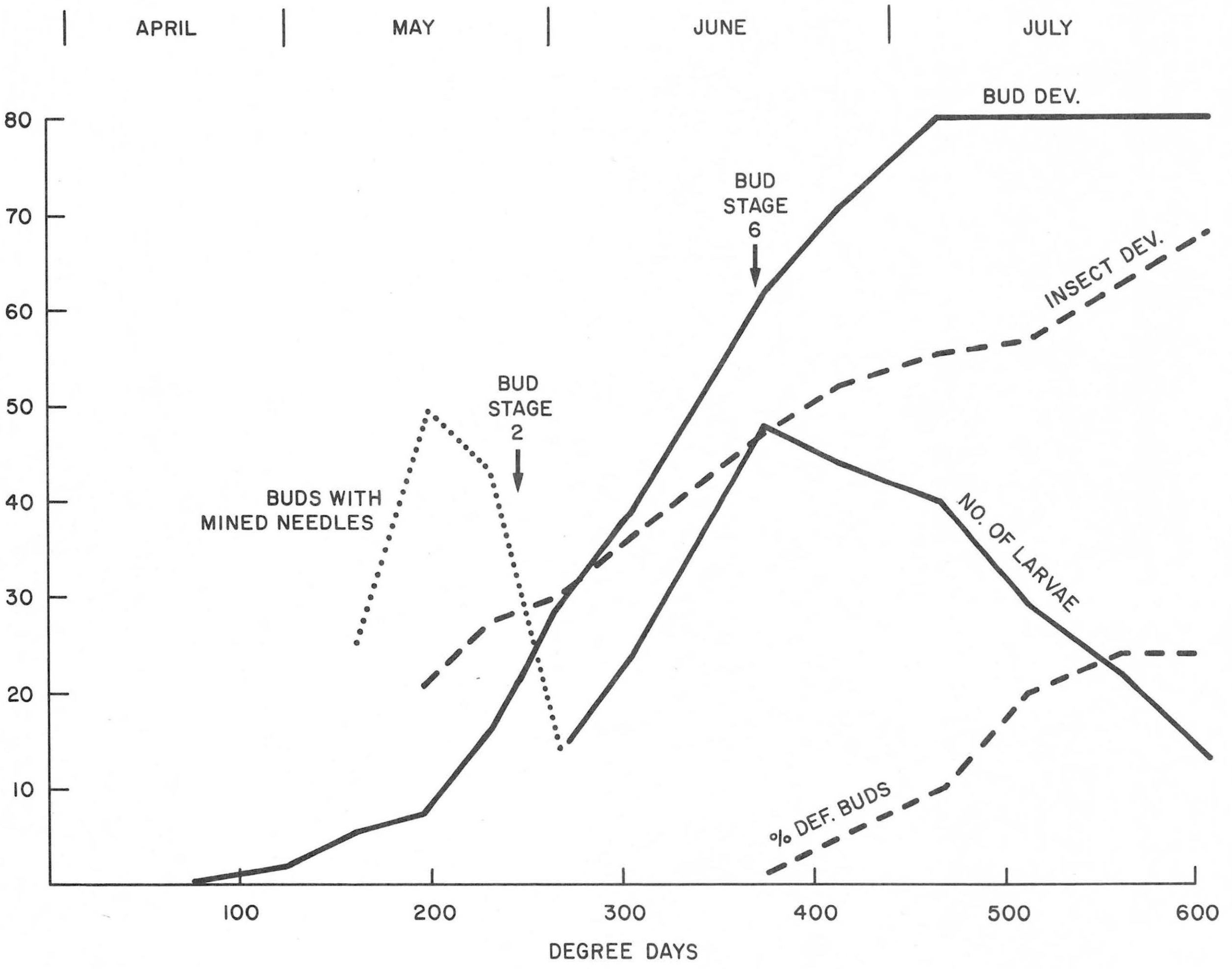

Figure 2. A comparative time series graph for the Hart Ridge, B.C., plot in 1980. Events recorded are bud developmental stage (0-8, X10) insect developmental stage (instar 2 to 6, X10 and pupae), larval density (per 100 buds), number of buds with mined needles (per 100 buds), percent of buds with >75% of the needles eaten.

enough so that larvae could penetrate the buds; average insect development stage was instar 2.9. Assuming one larva per newly mined bud, there was a decrease in larval numbers at this stage, presumably because all larvae could not find suitable buds. However, after bud stage 2 was reached, larval density slowly increased until June 20. This may have been caused by continued larval emergence from overwintering diapause and/or larval redistribution over the trees, thereby increasing the ranks in the buds under study. However, when buds reached stage 6 (372 degree days), the larvae lost their protective niches and their numbers began to decrease rapidly. Average insect development at this point was instar 4.8. By pupation (610 degree days), only 13 of the 48 present at stage 6 had survived.

Bud damage began as soon as larval penetration could be made at stage 2 and progressed steadily through until pupation (Fig. 2). Buds suffering 75% or more defoliation were noted first at 360 degree days and the percent of buds with this severity of attack reached 24% by the time of pupation. The final average defoliation in this plot was 57%, with 85% of the buds showing some damage.

This technique is most useful on a comparative basis and can be used to relate budworm survival to bud phenology sites, yearly weather or phenological races of trees.

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WESTERN LARCH AS A HOST OF THE WESTERN SPRUCE BUDWORM: A COMPARISON OF CAGED LARVAE ON SUSCEPTIBLE CONIFERS [1] [2]

Roy C. Beckwith

USDA Forest Service, Pacific Northwest
Forest and Range Experiment Station, Range
and Wildlife Habitat Laboratory, Route 2,
Box 2315, La Grande, Oregon 97850

Caged field studies indicate that the foliage of western larch is apparently less suitable to western spruce budworm larval development than the foliage of Douglas-fir, subalpine fir, and Engelmann spruce.

Western larch, Larix occidentalis Nutt., is sometimes listed as a major host of the western spruce budworm, Choristoneura occidentalis Freeman, (Furniss and Carolin 1977). Clearly, budworm larvae feed on larch and produce damage (Fellin and Schmidt 1967; Schmidt and Fellin 1973). However, numbers of eggs on larch are usually low suggesting that populations on this species stem partly from incidental oviposition but mostly from passive dispersal in the 1st and 2nd instars (Wissenbach 1982). Also, our observations have indicated, that although larch may support large numbers of early instars, few seem to survive to the pupal stage.

Large larvae from a laboratory colony were caged in the field on several of the listed host species to check the relative suitability of western larch as a host. Data were collected on survival and pupal weight when feeding was completed; this note reflects the results of that study.

Methods

Two field sites in north-central Washington were chosen to obtain four host species representing different genera. One site (B. S. Place) contained Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco, and larch; the other site (Twisp River) contained Douglas-fir, subalpine fir, Abies lasiocarpa (Hook.) Nutt., and Engelmann spruce, Picea engelmannii Parry ex Engelm. Douglas-fir was tested on both sites to be sure there were no major differences between sites.

At each site, five open-grown trees per species of approximately the same height (4-5 m) were selected for testing. Fine-mesh nylon bags were placed around 45-cm tips of four branches per tree about 2 m from the ground. To monitor temperature, one tree per species had thermocouples on the under-surface of branches within the nylon bags and on uncovered branches.

The nylon bags were stocked with laboratory-reared western spruce budworm.[3] The overwintering larvae had been exposed to cold temperatures to break diapause and timed to reach the 5th instar at about the same time as the field population. The test larvae were fed a standard budworm diet until they molted to the 5th instar, at which time they were randomly assigned to a specific nylon bag. Only five larvae were placed in each bag to ensure adequate current foliage to complete development. All cages at one field site were fully stocked within 2 days. Enough 5th instars were available at the proper time to infest five trees of Douglas-fir and Engelmann spruce at Twisp River; subalpine fir at Twisp River and the tree species at B. S. Place had four trees stocked with larvae.

Budworms in bagged branches were examined and temperatures from thermocouples recorded at 2- to 3- day intervals. Pupae were removed, sexed, and weighed to the nearest milligram within 72 hours of pupation. Pupal weight and survival were used to determine the adequacy of each host as a food source. Weights of naturally occurring pupae from Douglas-fir at B. S. Place were compared with those of pupae bagged on Douglas-fir at that site. Weights of only those pupae that successfully produced adults were used in the analyses. The data were analyzed by ANOVA; differences were tested by a Duncan's multiple range test (1955) incorporating Kramer's (1956) modification for unequal sample size.

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[1] Lepidoptera: Tortricidae.

[2] The research reported here was financed in part by the Canadian/United States Spruce Budworms Program - West.

[3] Supplied by Dr. M. Martignoni, Forestry Science Laboratory, Corvallis, Oregon.

Results

All individuals that survived to the pupal stage and emerged were pooled for each host in the analysis because survival and pupal weights were not significantly different between branches or trees.

Survival ranged from 49% on larch to 88% on Douglas-fir at Twisp River (Table 1). Survival on larch was clearly much lower than on the other species. The same pattern occurred when comparing pupal weights from the four hosts. Male and female pupae were significantly lighter on larch than on the other species (Table 2). The heaviest males were obtained from Douglas-fir at B. S. Place; the heaviest females were also obtained from Douglas-fir at B. S. Place, but they were not significantly heavier than those on Douglas-fir at Twisp River. In general, the bagged pupae on Douglas-fir were heavier than those collected from the natural population.

Table 1. Percent survival to adults of western spruce budworm reared on various hosts in north-central Washington, 1981.

Location	Host	Number Started	Number Adults	Percent Survival
Twisp River	Douglas-fir	100	88	88
	Subalpine Fir	80	67	83
	Spruce	100	82	82
B. S. Place	Douglas-fir	80	67	83
	Larch	80	39	49

Table 2. Pupal weights of western spruce budworm reared on different hosts in north-central Washington in 1981.

Location	Host	n	Males $\bar{x}$ (mg)[a/]	S.E.	n	Females $\bar{x}$ (mg)[a/]	S.E.
Twisp River	Douglas-fir	50	90.2 b	1.70	38	121.6 ab	4.75
	Subalpine Fir	35	76.4 c	2.13	32	91.3 d	2.92
	Spruce	45	80.8 c	3.10	37	108.3 bc	4.29
B. S. Place	Douglas-fir	46	103.9 a	2.70	21	135.5 a	5.45
	Larch	17	41.5 d	2.67	22	43.2 e	3.49
	Natural	26	81.6 bc	2.43	33	104.5 cd	2.73

[a/] Any two means by sex not having a common letter are significantly different at the .01 probability level.

Discussion

Reduced pupal weights and poor survival (49%) of western spruce budworm reared on larch may indicate that the foliage does not provide late instars with proper nutrition for normal development, or the foliage may contain materials that produce an antibiosis in the insect. Ryan (1979) found that survival and growth of the larch casebearer, *Coleophora laricella* (Hbn.), were associated with the stage of foliage growth. Under the conditions of the 1981 experiment, the laboratory stock may not have adapted as well to the larch foliage as to that of the other species. The report by Fellin and Schmidt (1967) of severe defoliation of larch does not mention when the damage occurred. The defoliation may have been caused by early larval feeding from high populations after spring dispersal (Beckwith and Burnell 1982). The rough bark of larch provides an excellent substrate for overwintering larvae that land on the trees during fall dispersal; large populations would thus be in place on the tree when the larvae emerge in the spring. Larch foliage breaks in the spring much earlier than Douglas-fir or true fir, thus new growth is available for early emerging larvae. The disappearance of larger larvae from larch could result from excessive predation, off-tree dispersal because of inadequate foliar nutrition, or both (Beckwith and Burnell 1982). Spur-shoot foliage apparently offers inadequate protection for large larvae. Preliminary work in 1980 also suggested that the foliage did not provide proper nutrition to produce pupae of normal size; however, larvae may still feed on the foliage as Chew (1980) found that larvae do not necessarily reject plants that fail to support larval growth in favor of those that do.

Why the natural pupae collected from Douglas-fir were significantly lighter than the caged insects on Douglas-fir is not clear. Feeding in the natural population may have been interrupted by predators, parasitoids or excessive wind movement. The experimental larvae may have been protected from these factors by the nylon mesh cages. The slightly different temperatures in the cages probably would not account for increased pupal weight; air temperatures in the cages were only 1 to 2°C higher when the cages were in the sun and equal to or slightly lower in shade. The artificial diet fed the first three instars of the test may have given them a growth advantage over the natural population. Also, the laboratory population may have larger pupae because of genetic differences.

A phytophagous insect must be able to complete its life cycle solely upon a plant species and be normal in all respects for that plant species to be considered a major host. An antibiosis response (delayed development, small size, or reduced fecundity) would indicate that the plant is marginal as a host (Painter 1968). Foliage of western larch is apparently less suitable to budworm development than foliage of Douglas-fir, true firs, and Engelmann spruce.

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SPRUCE BUDWORM AND ENERGY METABOLISM?

Thakor R. Patel

Biochemistry Department
Memorial University of Newfoundland
St. John's, Newfoundland A1A 3R3

ABSTRACT

The utilization of stored lipids (fat) for energy metabolism appears to be a fundamental process for many biological systems especially during the early stages of their development. The participation of the glyoxylate cycle (GOC) together with other metabolic sequences like gluconeogenesis and beta oxidation are necessary for the conversion of lipids to carbohydrates. This report describes the distribution of the GOC amongst biological systems and examines its importance to the development and existence of biological cells under different physiological conditions. The report also describes some of our work which focuses on the role of the GOC in non-parasitic (*Caenorhabditis elegans*) and parasitic (*Ascaris lumbricoides*) nematodes. It was possible to demonstrate the *in vivo* and *in vitro* inhibition of isocitrate lyase (ICL), a key enzyme of the GOC operating in these nematodes by itaconate. Finally this report explores the possibility of using target specific inhibitor like itaconate to control spruce budworm (*Choristoneura fumiferana*), populations.

Introduction

The spruce budworm is widely distributed in North America including Canada. The organism has been declared as an insect pest of national concern. It causes extensive defoliation and mortality to a wide variety of coniferous tree species including balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red spruce (*Picea rubens*), and black spruce (*Picea mariana*). Outbreaks of spruce budworm in Canada have been reported as early as 1700's (Blais, 1965). Timber losses in recent outbreaks when converted into dollar values amount to millions of dollars. Although the life cycle and the population dynamics of the spruce budworms have been explained no information is available on the biochemistry and physiology of the embryonating eggs and the developing larvae. The energy metabolism at the different developmental stages of the spruce budworm has not been examined. The examination of the energy metabolism of the embryonating eggs and the developing larvae of spruce budworm may result in information which may be used to come up with target specific inhibitors directed against the key enzymes of the GOC.

The Glyoxylate Cycle And Its Distribution In The Nature.

Kornberg and Krebs (1957) first revealed the evidence for the function of the GOC in replenishment of the tricarboxylic acid (TCA) cycle intermediates depleted during the glyconeogenesis and the amino acid biosynthesis. Its operation has been shown to be essential in cells which depend on acetate, ethanol, lipids, hydrocarbons and C_1 compounds for its carbon and energy needs (Cioni *et al*, 1981). Although the GOC was first described in bacteria utilizing acetate or ethanol as sole carbon and energy sources this pathway has a large representation in nature being operative under various nutritional and physiological phases of the life of many organisms.

The glyoxylate pathway can be described as a cyclic set of reactions starting from isocitrate and returning to it. This cycle (Fig. 1) allows the transformation of two acetate (as acetyl-CoA) into one of succinate. Five enzymes that participate in this catalysis include isocitrate lyase (ICL), malate synthase (MS), malate dehydrogenase (MDH), citrate synthase (CS) and acomitase (ASE). Reactions 1 and 2 (Fig. 1) immediately reveal the anaplerotic significance of the two enzymes (ICL and MS) as they produce two TCA cycle intermediates (succinate and malate) starting from one TCA cycle six-carbon compound (isocitrate) and a molecule of the substrate of the cycle (acetyl-coA). The glyoxylate cycle thus replenishes intermediates of the TCA cycle and conserves carbon that would otherwise be completely oxidized and lost to biosynthetic pathways. This replenishing function of the GOC has been termed 'anaplerotic'.

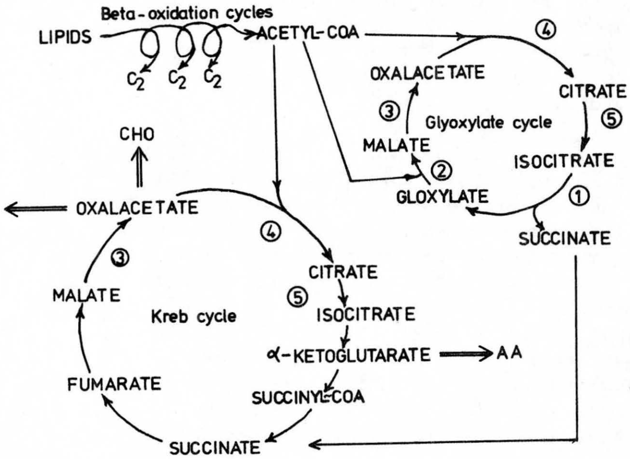

Fig. 1. Relationships between Krebs cycle, beta-oxidation and glyoxylate cycle. (AA = amino acid for biosynthesis; CHO = carbohydrates; C_2 = two carbon units, acetyl CoA).

The ICL has been found in bacteria (Woolfson and Krulwich, 1972; Ozaki and Shiio, 1968; McFadden and Howe, 1962, 1963; Sariaslani et al, 1961; Chell et al, 1978;), algae (John and Syrett, 1967; Haigh and Beevers, 1964a; 1964b; Dunham and Thurston, 1978; Collins and Merrett, 1975), pteridophytes (Gemmrich, 1979), gymnospermes (Firenzuoli et al, 1968; Vani et al, 1973), angiosperms (Gientka-Rychter and Cherry, 1968; Kagawa et al, 1973; Ihle and Dure, 1972; Theimer and Rosnitschek, 1978; Khan et al, 1977; Vani et al, 1979; Lango et al, 1975; Canvin and Beevers, 1961; Ford et al, 1976; Tester, 1976), fungi (Maxwell et al, 1975; O'Sullivan and Casselton, 1973; Flavell and Woodward, 1970; Reisener and Jager, 1967; Polakis and Bartley, 1965; Mendgen, 1973), protozoa (Hogg and Kornberg, 1963; Muller, Hogg and DeDure, 1968; Lovel et al, 1974), and nematodes and trematodes (Barrett et al, 1970, 1971; Colonna and McFadden, 1975; Rothstein and Mayoh, 1964, 1965, Prichard and Schofield, 1979; Patel and McFadden, 1977). The presence of the ICL has also been reported in the prepupae and pupae of the Prodenia eridania (Carpenter and Jaworski, 1962). It must be pointed out that the GOC has never been detected in animals more highly evolved than worms such as nematodes and trematodes.

The Physiological Role Of The GOC

In higher plants the GOC occurs in germinating seedlings of numerous plants where it is required for the conversion of stored lipids into carbohydrates which then form the source of energy during germination. In germinating spores of fern a similar lipid to carbohydrate transformation occurs. If one examines the levels of ICL and MS in the germinating fatty seeds a typical pattern is observed (Fig. 2). The increases in ICL and MS follow a simultaneous decrease in the total lipids in these seeds. The enzymes of the GOC are compartmentalized in single membrane, subcellular particles called 'glyoxysomes'. It must be noted here that glyoxysomes, unlike mitochondria, have a single bounding membrane.

In algae, the GOC participates in the utilization of acetate for growth when photosynthesis is not operative and carbohydrates are not available. The enzymes of the GOC have also been reported in the trematode, Fasciola hepatica (Prichard and Schofield, 1979), which is a mammalian liver fluke. In the case of Fasciola hepatica dults which live in the bile duct, it has been suggested that the GOC enzymes are involved in the production of glycogen to be incorporated into eggs which are very rich in glycogen (Horstmann, 1962; Wilson, 1967).

Although the data suggests that ICL and MS are scattered through out metazoan phyla, almost nothing is known about the function of this cycle in developing larvae and/or adult worms. Indeed only in the case of A. lumbricoides and C. elegans has the function of the GOC been clearly established (Rothstein and Mayoh 1965; Patel and McFadden, 1977, 1978, 1978b, 1978c). It has been shown that extensive synthesis of the disaccharide, trehalose, occurs in the developing embryos of A. lumbricoides at the expense of fat and that this conversion correlates with the appearance and disappearance of ICL and MS (Barrett et al, 1970). Quite recently Rubin and Trelease (1976) have found that the disaccharide resynthesis after embryonation accompanies the disappearance of triglyceride droplets found largely in the posterior half of the larvae. Dense microbody-like granules, restricted to the lipid-body region, are considered as possible subcellular sites for the enzymatic conversion of lipids to carbohydrates (Rubin and Trelease, 1977a, 1977b).

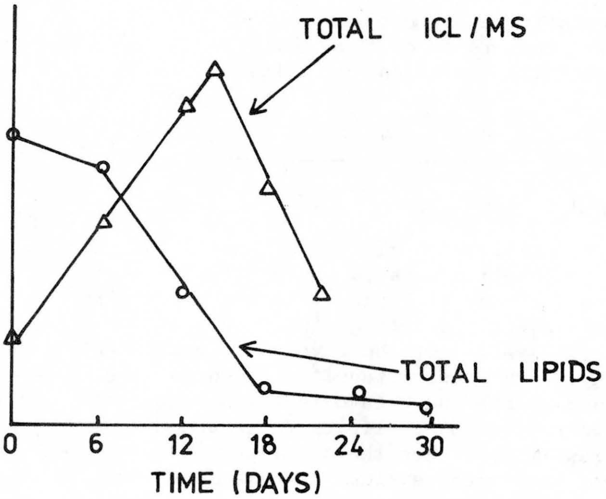

Fig. 2. Levels of MS and ICL (-△-) and total lipid (-○-) content during germination of seeds.

Materials And Methods

Materials. Succinic acid, itaconic acid, dithiothreiotol (DTT), glutathione (GSH), DL-isocitrate, morpholinopropanesulfonic acid (MOPS), beta-mercaptoethanol, Tris-HCl, and ethylene diaminetetraacetic acid (EDTA) were purchased from Sigma Chemical Co. Sephadex G-200 came from Pharmacia Fine Chemicals. All inorganic chemicals were commercially available and were of analytical grade.

Organisms And Growth Conditions.

Caenorhabditis elegans were kindly supplied by Dr. R.L. Russel, University of Pittsburgh, Pittsburgh, U.S.A. Escherichia coli K8-5m (CGSC strain No. 4868) is a mutant which fails to grow on acetate as a sole source of carbon and lacks isocitrate lyase when grown on glucose. The method for cultivation of C. elegans under monoxenic growth conditions has been reported earlier (Colonna and McFadden 1975; Patel and McFadden 1976).

Freshly recovered female Ascaris lumbricoides containing eggs were purchased from Nebraska Scientific Co., Omaha, Nebraska, U.S.A., shortly after preservation in 2% formalin. Eggs, obtained by removing the reproductive tracts from female worms, were embryonated for 22 days and treated with hypochlorite by the method described by Colonna and McFadden (1975) prior to breakage.

Preparation Of Crude Enzyme Extracts.

Crude extracts of C. elegans and A. lumbricoides were prepared by the methods of Patel and McFadden (1977).

Enzyme Assays

Isocitrate lyase was assayed at pH of 7.7 according to Roche et al (1971) with the inclusion of 0.2M phenylmethylsulfonyl fluoride (PMSF) in the assay buffer. Other enzymes of the GOC namely, malate synthase, citrate synthase, fumarase and catalase were also examined but will not be discussed here.

Protein concentrations in crude extracts were determined by the method of Lowry et al (1951).

Results

When washed eggs of A. lumbricoides were suspended in a solution of 0.1 N sulfuric acid and incubated on a shaker at 30°C ICL activity began to appear in the embryonating eggs on the eleventh day. It rearched a peak on day 18-20 and began to decline gradually thereafter. In the case of C. elegans the situation is slightly different. This non-parasitic nematode is self-fertilizing (hermaphroditic) worm living in soil where it feeds on bacteria. A fully grown worm measures about 1 to 1.5 mm in length. In a laboratory it can be cultivated just like bacteria using either axenic or monoxenic growth conditions. A single worm takes about 48 hrs from an egg stage to mature into a fully grown adult worm. During this short period it undergoes four molts representing the four larval stages, namely L_1 through L_4 (Fig. 3). Methods to obtain synchronous cultures of C. elegans have been described in our earlier report (Patel and McFadden, 1978).

The levels of ICL in the embryonating eggs and the larvae derived from them were monitored. The data in Figure 4 shows the specific activity of ICL was minimum in the zero-time sample representing unhatched embryonating eggs. The enzyme acitivity in the 48 and 60 hr samples was undectable. These samples contained young adult worms of uniform length bearing no eggs. These data suggest that ICL may have an important role in the biochemistry of the embryonating eggs and the young developing larvae, and that the adult organisms may not require the enzyme for its survival.

TIME (HOURS)		
0	HATCH, 600 SOMATIC CELLS, FURTHER GROWTH BY ENLARGEMENT OF THESE CELLS.	
6-11	FIRST LARVAL MOLT	L1 STATE
18	SECOND LARVAL MOLT	L2 STATE
26	THIRD LARVAL MOLT	L3 STATE
36	FOURTH LARVAL MOLT	L4 STATE ADULT
45-46	EGG LAYING BEGINS	
	4 EGGS PER HOUR INITIALLY	
	9 EGGS PER HOUR AFTER 92 HOUR.	
	EGG LAYING ENDS AFTER 120 HOUR.	

Fig. 3. Developmental stages in the life of Caenorhabditis elegans. (from Hirsch et al. 1976).

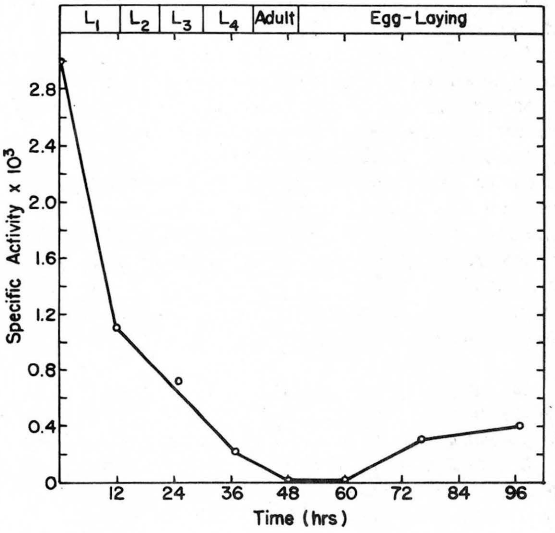

Fig. 4. Levels in ICL during synchronous growth of C. elegans larvae.

Itaconic acid (methylene succinic acid) was used as a target specific inhibitor to test in vivo and in vitro inhibition of ICL of A. lumbricoides. Figure 5 shows that itaconate inhibits the growth of C. elegans. At a 60 mM concentration the inhibitor caused 50% reduction in the growth of C. elegans in a random monoxenic culture of C. elegans. However, its effect on the growth of C. elegans in a random axenic culture was much pronounced. The results in Table 1 shows that 5, 30 and 60 mM itaconate caused 70, 93 and 99% inhibitions, respectively.

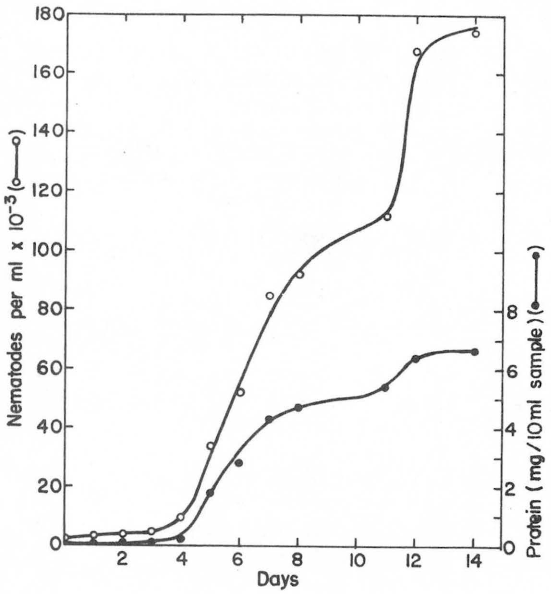

Fig. 5. Growth inhibition of C. elegans by itaconate (60 mM) in monoxenic cultures.

Table 1. Growth of C. elegans in the presence and absence of metabolic inhibitors[a].

		Worms/ml x 10^{-3}					
Day	Control	Itaconate			Oxalate	Maleate	Succinate
		10 mM	30 mM	60 mM	10 mM	10 mM	10 mM
1	3.8	3.8	3.8	3.8	3.8	3.8	3.8
3	9.1	7.2	6.0	3.2	8.0	8.8	8.9
5	64.7	32.1	13.8	6.3	51.5	32.0	67.9
7	162.0	106.2	22.5	9.2	146.9	139.0	175.0

[a] Each 250-ml flask contained 15 ml of axenic medium plus one of the above filter-sterilized compounds. Worm counts were made by direct microscopic examination as described. All the flasks were shaken at 120 rpm and 23°C in a Psychroterm incubator.

In order to test the specificity of itaconate inhibition of growth of C. elegans other compounds shown in Table 2 were tested. Itaconate in a 10, 30 and 60mM concentrations resulted in 34, 86 and 94% inhibitions, respectively. In contrast, oxalate and maleate caused negligible inhibition of the growth of C. elegans while succinate showed a stimulatory effect. The effect of itaconate upon the growth of synchronously growing monoxenic culture of C. elegans was maximum. In this case the inhibition is almost 100% (Fig. 6). This is not unexpected since itaconate may inhibit ICL in embryos and L_1 larvae of C. elegans. This result compliments nicely the earlier observation in which it was shown that ICL level is higher during embryogenesis and L_1 larvae stage after eggs were allowed to hatch in a monoxenic medium (Fig. 4).

Table 2. Effect of itaconate on the growth of C. elegans.[a]

	Worms/ml x 10^{-3}				
Days	Itaconate				
	0.0 mM	5 mM	15 mM	30 mM	60 mM
0	0.40	0.4	0.40	0.40	0.40
2	0.60	0.46	0.26	0.20	0.20
5	2.80	2.06	1.60	0.60	0.20
6	8.60	2.52	1.87	0.60	0.20
8	12.00	7.00	3.40	2.40	0.20
10	41.00	12.66	–	2.80	0.27

[a] Each of the 500-ml Erlenmeyer flasks contained 60 ml of axenic medium with the indicated concentrations of itaconate. The flasks were inoculated with 0.5 ml of a random population of C. elegans, and incubated on a shaker in a Psychroterm drawn from each flask at the given times to determine the worm population as described in MATERIALS AND METHODS.

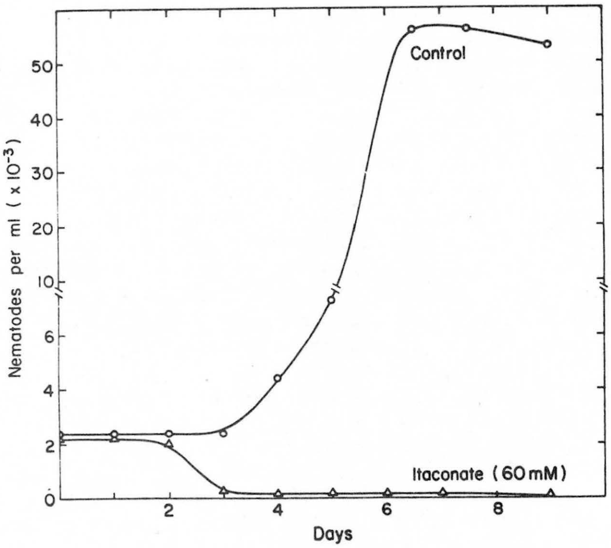

Fig. 6. Effect of itaconate (60mM) on the synchronous growth of C. elegans in a monoxenic culture.

Increasing concentrations of itaconate caused higher in vitro inhibition of ICL in crude extracts of C. elegans (Fig. 7). More than 80% inhibition was observed with 10 nanomolar concentrations of itaconate. A similar pattern of inhibition was also observed with ICL in crude extracts of A. lumbricoides. Kinetic studies using the enzyme from both the organisms (C. elegans and A. lumbricoides) indicate itaconate is a non-competitive inhibitor of ICL. The apparent inhibition constants were 19 micromolar for C.

elegans enzyme and 7.3 micromolar for *A. lumbricoides* enzyme.

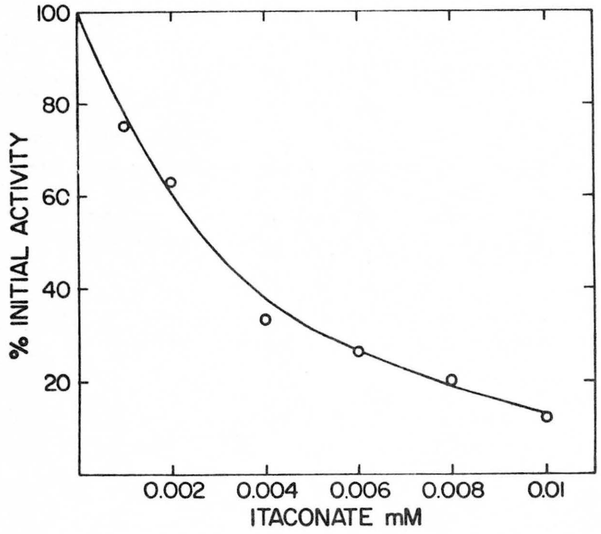

Fig. 7. *In vitro* inhibition of ICL of *C. elegans* by itaconate.

Discussion

The above results indicate that GOC cycle plays an important role in the biochemistry of embryonating eggs and the young developing larvae of *C. elegans* and *A. lumbricoides*. In the case of *C. elegans* it was possible to demonstrate that itaconate acts as a specific inhibitor of ICL *in vivo* as well as *in vitro*. The inhibitor caused drastic reduction in the population of the nematodes in monoxenic and axenic cultures.

An important question is raised here. Is it possible to employ target specific inhibitor like itaconate or other such compounds to blockade the GOC and hence prevent the growth of an organism? The answer is yes. The experiments described above suggest that itaconate may be used as a target specific inhibitor to prevent the growth of nematodes like *C. elegans*.

The work in McFadden's laboratory showed that ICL in crude extracts of *Ps. indigofera* and *N. crassa* were inhibited by itaconate, an analogue of succinic acid. The enzymes of the bacterial and the fungal sources have been purified to homogeneity. The inhibition studies using the purified enzymes indicated that itaconate is a competitive inhibitor with respect to succinate in the condensation (or reverse) reaction and is uncompetitive with respect to glyoxylate. In the forward (cleavage) reaction the itaconate acted as a non-competitive inhibitor. In the present study itaconate was found to be non-competitive inhibitor when ICL from *C. elegans* and *A. lumbricoides* were tested.

Recently Bruce McFaddens group at Washington State University, Pullman, have shown that itaconate can bring about *in vivo* inhibition of *Pseudomonas indigofera* growing on acetate. The results obtained with cultures of *C. elegans* compliment their finding. The inhibition of isocitrate lyase by itaconate in the case of *Tetrahymena pyriformis in vitro* and *in vivo* has been reported by Dang and Cook (1981).

If one examines the life cycle of the spruce budworm one finds some interesting features which raise important practical questions. In Newfoundland in late July or early August the moth lays eggs which embryonate and hatch into first instar larvae in about ten days. These larvae do not feed but are very active, moving on branches or hanging by their silky threads. They soon begin to look for a place in preparation for wintering over. They prepare hybernacula in which the second instar larvae winter over. These larvae hibernate until the arrival of the spring in May or early June. The second instar larvar become active and undergo molting to complete the remaining developmental stages to produce sixth instar larvae. The pupation occurs in July and August. The young moth appears and begins to lay eggs shortly thereafter.

There is some similarity in the early developmental stages in the life of *C. elegans* and the spruce budworm. Perhaps they resemble in theirtheir biochemistry and physiology during their early stages. If this is true then it may be possible to use itaconate as a target specific inhibitor to prevent the progress in the development of the larval stages of the spruce budworm. Before such practical approach is adopted it is necessary initially to do some fundamental research to investigate the biochemistry and physiology of the embryonating eggs and developing larvae of spruce budworm.

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COMPARISONS OF ELEMENTAL PROFILES OF THE WESTERN SPRUCE BUDWORM[1] REARED ON THREE HOST FOLIAGES AND ARTIFICIAL MEDIUM.

John A. McLean, P. Laks, and T.L. Shore[2]

Faculty of Forestry, University of British
Columbia, 2357 Main Mall, Vancouver, B.C.
Canada V6T 1W5

Western spruce budworm were reared on three host foliages and artificial medium. Trace element analyses showed large differences in elemental concentrations between food sources and only minor differences between insect life stages. Discriminant analyses were carried out to test the distinctiveness of adult chemoprints from each rearing regime. Fe, Cu, and Zn were distributed differentially between egg mass and other parts of the female moths. Females reared on artificial medium weighed more than foliage-fed females.

Introduction

The usefulness of a trace element "chemoprint" of an insect, as determined by simultaneous multi-elemental analytical techniques such as X-ray energy-dispersive spectrometry (XES) (Bertin 1978), has relied on a basic assumption that the elemental profile of an insect reflects its host plant and thus indirectly the soil and bedrock geology. The western spruce budworm, *Choristoneura occidentalis* Freeman, has been shown to have a sufficiently distinctive area specific chemoprint to distinguish adults from two stands 2.6 km apart (McLean *et al*. 1979). In addition, considerable among tree variation was also reported. The objective of this study was to determine if there was significant variation between the chemoprints of western budworm reared on three host foliages, Douglas-fir (DF), *Pseudotsuga menziesii* (Mirb.) Franco, Engelmann spruce (ES), *Picea engelmannii* Parry, Grand Fir (GF), *Abies grandis* (Dougl.) Lindl., and artificial medium Bio-Mix #9769 . Quantitative data were developed in this study to overcome legitimate criticisms raised on the reliability of elemental assignments in earlier studies of salmon, snowgeese and ambrosia beetles using X-ray energy spectrometry (Bowden *et al*. 1979).

Methods

Fourth instar western spruce budworm (WSBW) larvae were collected on hand clipped from infested trees at Oregon Jack Creek, British Columbia, in June 1978. These larvae were laboratory-reared on new DF, ES and GF foliages as well as artificial medium. The DF and GF foliage were collected fresh from the U.B.C. Endowment Lands as required. The ES foliage was collected from Rhododendron Flats in Manning Park B.C. and stored at 3°C until required. Samples of new (less than 4 months old) and old (more than a year old) foliage, male and female WSBW pupae and adults of both sexes were collected from each rearing regime and freeze dried.

A subset of larvae were assigned randomly to one of the four rearing regimes and reared individually through their fifth and sixth instars. Weight measurements were taken within 24 hours of moulting. Adults were allowed to mate in pairs, egg counts were made, and percentage hatch determined.

Samples for XES analysis were mixed with Somar Mix®[4] in a ratio of 2 parts sample: 1 part Somar-Mix and thoroughly ground in a SPEX[5] mill for five minutes. Two 60 mg self-supporting 13 mm diameter pellets were made in a KBr die at a pressure of 1000 kg. Quantitative programs were developed using standard addition techniques on bulked DF foliage and female WSBW material. Checks were made against U.S. National Bureau of Standards (NBS) orchard leaves (# 1571) and NBS bovine liver (# 1577).

All XES analyses were carried out by irradiating each pellet with Mo-filtered X-rays produced by a Mo X-ray tube at 35 keV and 0.2 Ma for 400 sec. The count rate of the emitted X-rays was 20K cps and they were detected by a

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[1] *Choristoneura occidentalis* Freeman Lepidoptera: Tortricidae)

[2] Present address: Pacific Forest Research Centre, 506 West Burnside Road, Victoria, B.C. V8Z 1M5

[3] Bioserv Inc. Frenchtown, N.J.

[4] Somar Laboratories Inc., New York, N.Y.

[5] SPEX Industries Inc., Metuchen, N.J.

Si-Li drifted detector which had a 185 eV resolution at 5.895 keV. The general apparatus has been described by D'Auria and Bennett (1975).

Three pellets of pure Somar-Mix were also analysed with each group of samples to provide an average "background" spectrum. This was proportionalized to the analyte spectrum and subtracted to produce a spectrum with a minimum of background. Regions of interest were defined on this background subtracted spectrum to obtain the number of counts for each element being considered. Each region of interest was expressed as a proportion of the Compton backscatter peak (before background subtraction) of the analyte spectrum for derivation of the quantitative proportionalities. A detection limit was assigned at the point where the negative confidence interval (P = 0.05) of the calibration curves intersected the X-axis, i.e. the point where the normalized variable computed from the XES spectrum was equal to the confidence interval.

Samples of artificial medium, new and old foliage, pupae and adults of both sexes from each rearing regime were analysed for K, Ca, Mn, Fe, Cu, Zn, Br, As, Rb and Sr. An additional experiment was carried out to determine if these same elements were equally distributed between egg masses and the residual body of female WSBW from the AM rearings. For this study one group of five samples of five females each were freeze dried and analyzed to determine the overall ppm of each element. In a second group, five samples of five females each were taken, anaesthetized with CO_2, the ovaries and associated tissues removed from abdomens and the composited samples of the five egg masses and five residual carcasses freeze dried prior to XES analysis.

Comparisons of elemental data among life stages, and among whole insects, egg masses, and skeletons, were carried out using ANOVA in MIDAS[6]. Stepwise discriminant analysis, BMD: P7M (Jennrich and Sampson 1977), was used to test whether the elemental profiles of the insects reared from each host foliage and the artificial medium were distinct.

Results and Discussion

The WSBW feed primarily on new foliage. They are voracious feeders and the majority of their consumption of foliage occurs during the fifth and sixth instars (Brown 1973). During

TABLE I: Comparison of elemental levels in new and old foliages of the Douglas-fir, Engelmann Spruce and Grand Fir, used to rear the WSBW

Element	ppm[a]					
	Df		ES		GF	
	Old	New	Old	New	Old	New
K	4106b	7300a	5800b	17000a	5000b	11400a
Ca	9700a	5017b	12706a	2103b	10145a	6100b
Mn	104.0a	80.3b	540.4a	124.8b	593.7a	244.1b
Fe	99.8a	58.6b	202.5a	28.6b	34.0a	12.1a
Cu	0.2a	1.6a	10.0a	7.6a	2.6a	0.4a
Zn	4.9a	13.2a	69.4a	42.9b	24.2a	26.4a
As	6.5a	1.5a	4.3a	0.4a	2.4a	0.3a
Br	18.0a	10.4a	10.8a	15.0a	7.4a	7.1a
Rb	5.5a	7.9a	7.0b	11.6a	9.2b	22.3a
Sr	53.7a	24.8b	82.4a	15.2b	50.6a	28.4b

[a] Means within each element by host category followed by the same letter not significantly different, t-test, P<0.05

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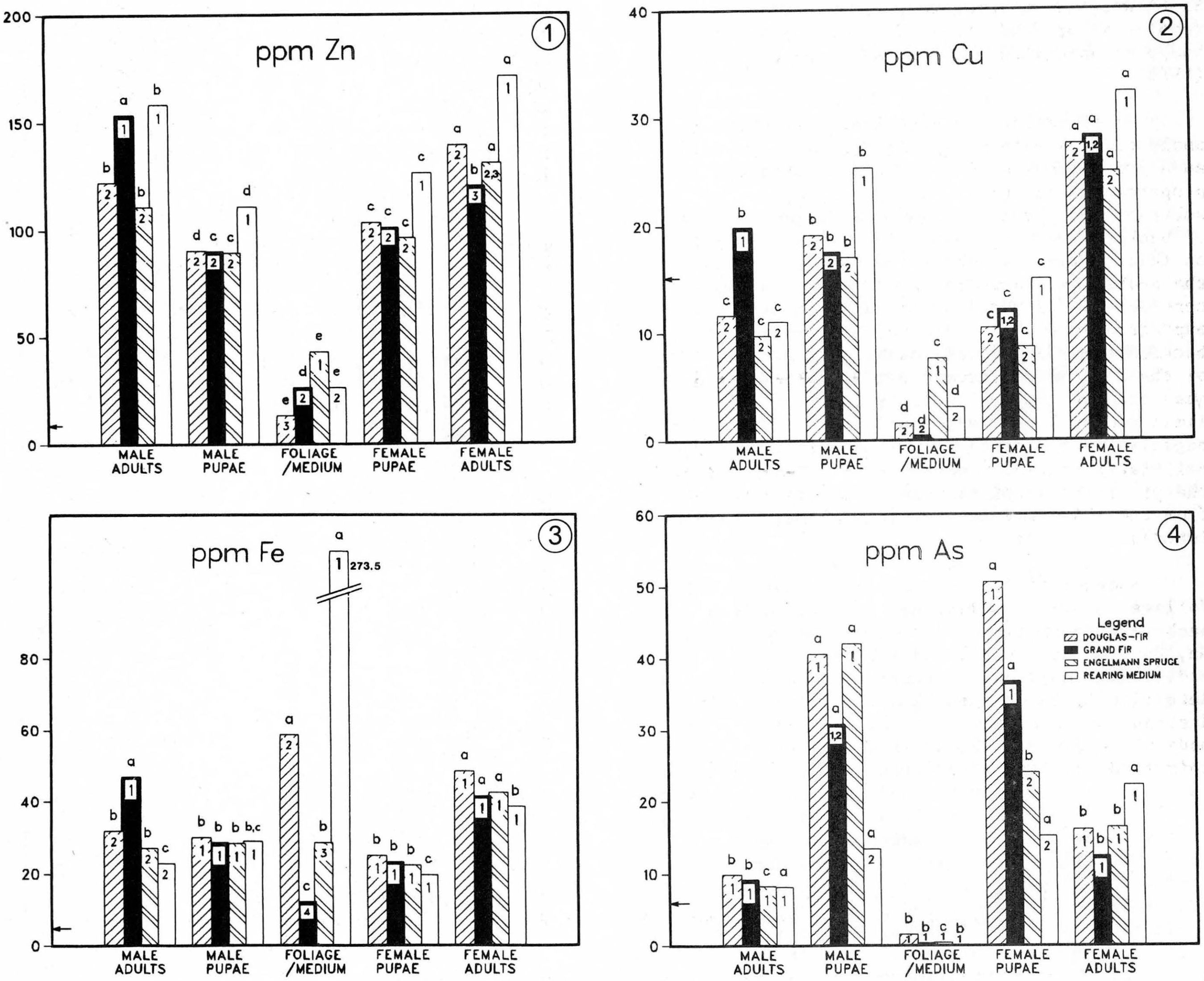
[6] Michigan Interactive Data Analysis System (Fox and Guire 1976).



FIGURES 1-4: Results of the study showing levels of elements in western spruce budworm pupae and adults reared from three host foliages and artificial medium.

NOTE: Letters above bars indicate significant differences among life stages reared on each host; numbers within bars indicate significant differences within the same life stages taken from each rearing regime, Scheffe's Test, P<0.05; detection limit indicated by horizontal arrow on Y-axis.

this period, tremendous growth takes place. For these reasons it was assumed that there would be sufficient opportunity for the different food sources to produce an effect on the elemental profile of reared pupae and adults. There were wide differences in element concentrations between new and old foliage with higher concentrations of K in all new foliages and higher Rb levels in new foliage for ES and GF. There were lower concentrations of Ca, Mn, Fe (except for GF) and Sr in new foliage as compared to old foliage (Table I). The remaining elements (Cu, As, Br) did not vary in concentration between old and new foliage except Zn which showed a minor variation with higher levels in old ES foliage.

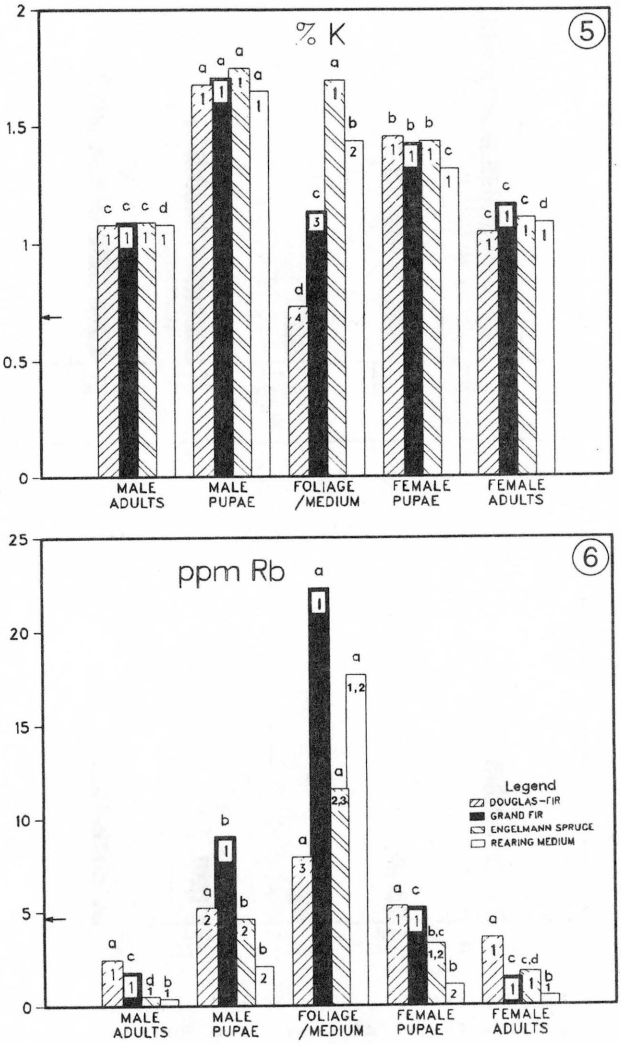
Two of the important enzyme co-factors in living tissue, Zn and Cu, showed elevated levels in WSBW pupae and adults as compared to the new foliage (Figs. 1, 2). Even though ES foliage had the highest Zn levels amongst the foliages and AM, it was the insects reared on the artificial medium which had highest levels. Zn levels were similar in male and female pupae but there was considerable variation among the adults (Fig. 1). A similar pattern of increasing Cu levels was found from new foliage to female pupae and female adults. Although Cu levels of male pupae were elevated, they decreased during metamorphosis to the adult (Fig. 2). No explanation can be given for this phenomenon. It should also be noted that neither the oxidation state nor the chemical environment of the element in the insect is determined during XES analysis. Levels of Fe varied widely among foliages and artificial medium but all pupae had similar concentrations (Fig. 3). Adults also had similar levels except GF male WSBW reared on GF which had higher Fe levels than other males. These results suggest that Fe is probably under homeostatic regulation.

Highly variable levels of As were found in the insect life stages even though concentrations in the foliage and AM were extremely low (Fig. 4). Accumulations of these high levels suggest bioaccumulation may have occurred in the field before the laboratory rearing was undertaken. There was a significant decrease in As concentrations in the emerged adults.

Levels of the important macronutrient K were significantly different among the rearing medium and new foliages (Fig. 5). The levels within each life stage were not significantly different, suggesting that this element is also under homeostatic regulation. Levels in adults were significantly less than those of the pupae. A potassium substitute of some interest is Rb and it has been used as a marker element for dispersal studies (see recent review by Raulston 1979). The levels of Rb in the foliages and AM were relatively low and there were decreasing levels recorded in pupae and adults (Fig. 6).

The elements Ca and Sr were present in comparatively high concentrations in the foliages and artificial medium but only small amounts were taken up by the insects (Figs. 7, 8). Br levels, on the other hand, have undergone bioaccumulation, especially in those insects reared on DF and GF (Fig. 9). It is possible that salt spray accumulated on foliage samples collected from the University Endowment Lands and that once Br was within the larvae it was not excreted. Of all the elements, Mn was one of the most abundant in foliage samples but was barely detectable in the WSBW life stages (Fig. 10). It would appear that this element is either not taken up or is rapidly excreted by the WSBW.

How was the development of the WSBW affected by the various diets? The larvae which fed on the artificial medium showed greater weight gains in the females at all life stages (Table 2). There were no significant differences in weight gain (as a proportion of L6 weight) for male pupae or adults (Table 2) among food sources. The numbers of eggs laid by females reared on the host foliages were similar although significantly fewer eggs were laid by females reared on AM. Percentage hatched was also significantly greater for the eggs from the three host foliage reared females (Table 2). These results suggest that mating may not have been successful for the insects reared on artificial medium.



FIGURES 5-6: Results of western spruce budworm rearing study showing variations in elemental concentrations among host foliages and insect life stages. See note on Figs. 1-4 for explanation of significance levels indicated.

TABLE 2: Summary of development data for field collected western spruce budworm reared on new foliages of three host tree species and artificial medium

Stage[b]	Males				Females			
	DF[a]	ES	GF	AM	DF	ES	GF	AM
Live weight (mg)								
Initial L6 weight	25.3	40.4	46.3	31.1	40.5	66.9	54.0	41.7
(No.)	(6)	(4)	(5)	(4)	(3)	(6)	(6)	(7)
Live weight as a proportion of L6 weight								
Initial pupal weight	2.9a	2.5a	1.8a	3.0a	1.9b	2.2b	1.9b	5.0a
Final pupal weight	2.5a	2.0a	1.5a	2.6a	1.6b	2.1b	1.7b	4.4a
Adult weight	1.5a	1.5a	0.8a	1.5a	1.2b	1.4b	1.2b	3.4a
Fecundity (eggs per female)					120.8ab	143.3a	102.8ab	68.4b
(n)					(10)	(9)	(9)	(9)
Mean percent hatch					98.6a	91.2a	89.4a	32.1b

[a] Hosts indicated as DF = Douglas-fir, ES = Engelmann Spruce, GF = Grand Fir and AM = artificial medium.

[b] Weights determined within 24 hours of moulting to minimise variation resulting from feeding.

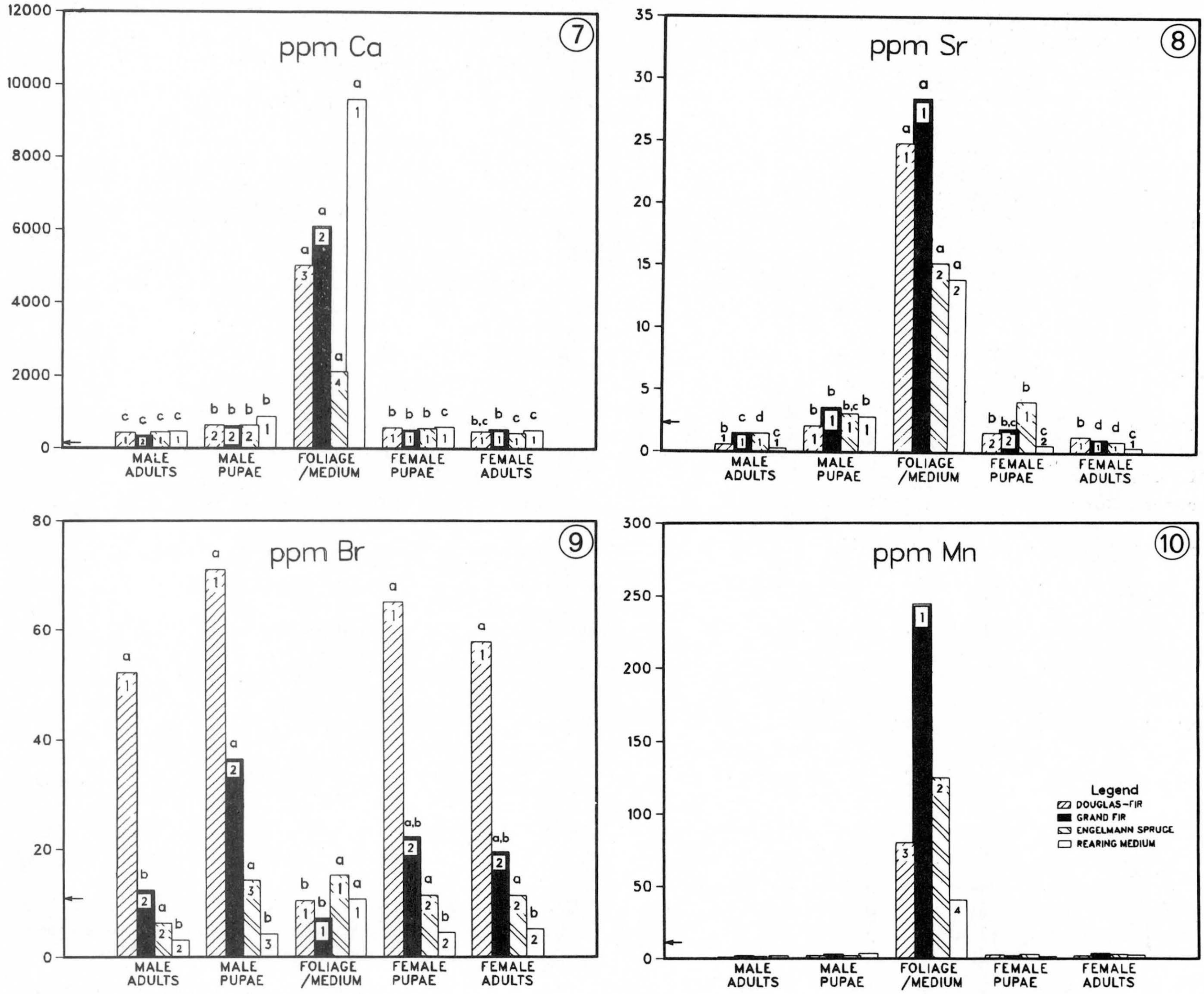
Comparisons of the levels of Fe, Cu, and Zn in carcasses and egg masses showed higher Fe and Cu levels in the carcasses and higher Zn levels in the egg masses (Table 3). Thus, the amount of oviposition by females will affect residual levels of these elements which could be of consequence in population studies of female WSBW involving chemoprinting. Fluctuations associated with oviposition or feeding may be circumvented by using a portion of the body not associated with oviposition such as a wing as Turnock _et al._ (1980) suggested in their study of the red turnip beetle, _Entomoscelis americana_ Brown. In retrospect a more reliable chemoprint for female WSBW might be obtained by removing abdomens before analysis.

In the discriminant analysis of males from the four rearing regimes, 16/17 (94%) were correctly assigned to their feeding group in the jackknife classification procedure (Table 4). All group means were significantly separated from each other. For the females, the problem of partitioning Zn, Fe and Cu between carcasses and egg masses was allowed for by designating these elements a "secondary" set in the discriminant analysis. This required that selection of significant variables be made from among the other seven elements first and only when none of these met the criterion for entry (F = 4.0) would selection be made from the secondary set. In this case, the results were identical with and

TABLE 3: Comparisons of Fe, Cu and Zn levels in whole insects, egg masses and residual carcasses of WSBW reared on artificial medium

Element	ppm ($\bar{x} \pm$ s.d., n=5)[a]		
	Whole Insect	Skeleton	Egg Mass
Fe	27 ± 3b	49 ± 5a	20 ± 5c
Cu	12 ± 3b	22 ± 7a	7 ± 4b
Zn	153 ± 9ab	132 ± 18b	168 ± 31a

[a] Means within rows followed by the same letter, not significantly different, P<0.05, Scheffe's Test.



FIGURES 7-10: Results of the study showing levels of elements in western spruce budworm pupae and adults reared from three host foliages and artificial medium. See note with Figs. 1-4 for explanation of significance levels indicated.

without the designation of a secondary set of elements with only Zn and Br being included in the discriminant function. The only group means not statistically distinct were those of female WSBW reared on the ES and GF. (Table 5). In the jackknife classification procedure only 11/18 (61%) of the females were correctly assigned to rearing regime.

House (1974) reviewed the roles of minerals in insect nutrition tabulating data for Ca, Cu, Fe, K and Zn (of the elements considered in this study). He also described the area of mineral requirement of insects as probably the most neglected area of research in insect nutrition. Quantitative multi-elemental procedures, such as XES, will add greatly to our understanding of normal element concentrations and allow us to more fully appreciate the normal homeostatic mechanisms operating during an insect's metamorphosis and will also, hopefully, indicate which elements are suitable for geographical characterization of populations. Three promising candidates appear to be As, Br and Rb. Some of these, especially Rb, might be manipulated to mark a forest defoliator population, as has been done with several agricultural insects (Raulston 1979). More reliable chemoprinting results for female WSBW might be obtained by removing abdomens prior to analysis and by so doing avoid variations related to ovipositon.

TABLE 4: Results of discriminant analysis of male adult WSBW reared on Douglas-fir, Grand Fir and Englemann Spruce foliages, and artificial medium (DF, GF, ES and MED respectively)

Step Variable Entered	Coefficients for Canonical Variable 1	Coefficients for Canonical Variable 2	Element
1	-0.21	0.22	Br
2	0.12	-0.06	Fe
3	0.11	0.06	Zn
Constant	-11.18	-0.18	

Eigenvalues: 7.82, 6.78

Cumulative proportion of total dispersion: 0.47, 0.88

Canonical Correlations: 0.94, 0.94

Matrix of F-values for testing group means:

Group	DF	GF	ES
GF	15.09**		
ES	27.30**	10.72**	
AM	23.20**	24.54**	24.20**

Jackknife classification matrix:

Origin of Moths	No. Classified as DF	GF	ES	AM	Total
DF	5	0	0	0	5
GF	0	4	1	0	5
ES	0	0	5	0	5
AM	0	0	0	2	2

94.1% of calibration group correctly assigned to host food source.

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[a] Probability level indicated, ** = P < 0.01

Acknowledgements

We thank E. Hoffman, J. Holman, G. Shrimpton and J. Thorburn for their assistance in the field; R.F. Shepherd and T. Gray for advice on rearing and for the loan of equipment. We thank R. Shepherd and Y. El-Kassaby for helpful comments on early drafts of the manuscript. This research was supported by funds from CANUSA-West and NSERC operating grant A0462.

TABLE 5: Results of discriminant analysis of female adult WSBW reared on foliage from Douglas-fir, Grand Fir, Engelmann Spruce and artificial medium (DF, GF, ES and AM respectively)

Step Variable Entered	Coefficients for Canonical Variable 1	Coefficients for Canonical Variable 2	Element
1	-0.08	0.03	Zn
2	0.01	0.07	Br
Constant	11.15	-5.47	

Eigenvalues: 3.35, 2.40

Cumulative proportion of total dispersion: 0.58, 1.00

Canonical Correlations: 0.88, 0.84

Matrix of F-values[a] for testing group means:

Group	DF	GF	ES
GF	11.38**		
ES	13.08**	0.96	
AM	17.65**	18.43**	13.03**

Jackknife classification matrix:

Origin of Moths	No. Classified as DF	GF	ES	AM	Total
DF	2	1	1	0	4
GF	1	3	0	0	4
ES	2	1	2	0	5
AM	1	0	0	4	5

61.1% of calibration group correctly assigned to host food source.

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[a] Probability level indicated, ** = P < 0.01

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CHEMICAL BASIS OF HOST PLANT SELECTION BY EASTERN SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* CLEM. (LEPIDOPTERA: TORTRICIDAE)

P.J. Albert and S. Parisella

Department of Biology,
Concordia University,
7141 Sherbrooke St. W.,
Montreal, Quebec
Canada, H4B 1R6

The epicuticular waxes from four host plants of the eastern spruce budworm are examined with respect to their influence on the feeding behavior of the sixth-instar larva. Both current and one-year old needles contain stimulating chemicals in their epicuticular wax layer. Some pure fatty acids known to occur in balsam fir wax are stimulatory, and may serve to enhance the already strong feeding response to sucrose.

Introduction

The feeding responses of eastern spruce budworm larvae toward various pure chemicals and some extracts from white spruce were first studied by Heron (1965). Their responses to polar and non-polar compounds from a number of evergreen plants were studied by Albert and Jerrett (1981) who showed that the sugar/glycoside fraction from balsam fir was more stimulating than either amino acids or organic acids from the same host. Subsequently, Albert et al. (1982) characterized the feeding responses to pure carbohydrates, and reported that sucrose was the most stimulating of the sugars tested. Sucrose is known to play an important role in the feeding behavior of many insects (Dethier, 1966). In spruce budworm larvae, the peak response to sucrose is in the range from 0.01 to 0.05M, with a behavioral threshold at 10^{-4} to 10^{-3}M, indicating a high degree of sensitivity to this chemical (Albert et al., 1982).

Using four of the more common host species in eastern North America (balsam fir, white, black and red spruces), Albert (1983) found that the sugars/glycosides from all four hosts were highly stimulating to spruce budworm larvae. Amino acids were only slightly stimulating while organic acids were neutral or deterrent. Lipids from white and red spruces were more stimulating than those from balsam fir and black spruce. This fraction from white spruce was found to be even more stimulating than the sugars/glycosides.

The first stage in the feeding behavior of many phytophagous insects involves the "test biting" of the leaf surface, a process which may be initiated as a result of the stimulation of peripheral sensilla by material contained in the epicuticular wax layer of the plant leaves (Bernays et al., 1975). Simple observations in our laboratory showed that a larva crawling on the surface of a fresh shoot of balsam fir would palpate the surface of the foliage with its maxillae, and bite into the leaf within a few seconds. Larvae given foliage treated with hexane to remove the epicuticular waxes spent considerable time palpating the surface without biting. The present study examines the feeding responses of spruce budworm larvae to surface chemicals from four host plants and to some pure fatty acids known to occur in balsam fir wax (Beri and Lemon, 1970).

Materials and Methods

Sixth-instar larvae were used in two-choice tests as described previously (Albert et al., 1982). Control discs were impregnated with 15µl of hexane which was allowed to evaporate. They were then wetted with 15µl of distilled water. Test discs were impregnated with 15µl of a solution of epicuticular waxes in hexane. The solvent was allowed to evaporate and the discs were then wetted with 15µl of distilled water.

Extracts of epicuticular waxes were obtained from balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and red spruce (*Picea rubens*). These were prepared by dipping 10g of "fresh" needles (from frozen samples which were collected on June 14, 1982 from the Acadia Forest Experiment Station, N.B.) in 200 ml of glass-distilled hexane for 30 sec. The solvent was evaporated and the extracted material was re-dissolved in 3 ml of hexane to provide the stock solution for the behavior tests.

Some fatty acids were tested at a concentration of 10^{-3}M. Those which proved stimulating were further tested in combination with sucrose (0.025M), using 0.025M sucrose on the control discs.

Data are presented either as mean % consumption ($\pm$S.E.) of test versus control discs, or as a preference index (PI=(T-C)/H, where PI is the preference index, T is the amount eaten of the test discs, C is the amount eaten of the control discs, and H is the time in hours). Multiplying the PI by 33.183 yields the difference in disc area (mm^2) eaten between test and control discs per hour.

Results and Discussion

The feeding preferences for discs containing extracts of epicuticular waxes from host plants versus control discs are shown in Figure 1. All four hosts' waxes contain stimulatory chemicals which presumably serve as biting stimuli.

FIGURE 1. Mean % consumption (± S.E.) of discs treated with hexane extract and with water in two-choice tests.

H_2O : Water Controls
BF : Balsam fir
WS : White spruce
BS : Black spruce
RS : Red spruce

(N) : Current year's growth
(O) : 2-year-old growth

N : Number of experimental animals
P : Probability values; Wilcoxon's Signed-Ranks Test

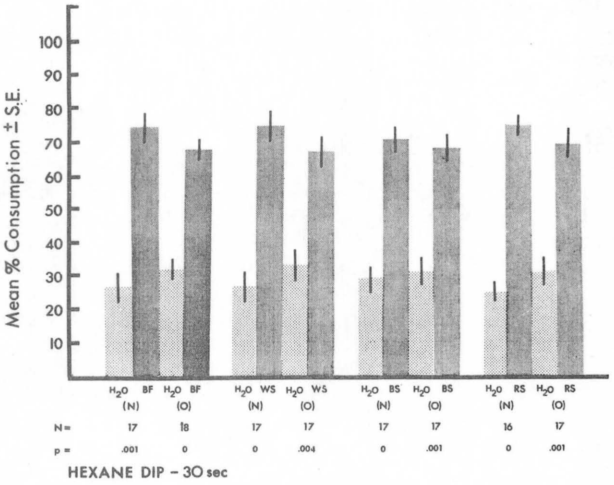


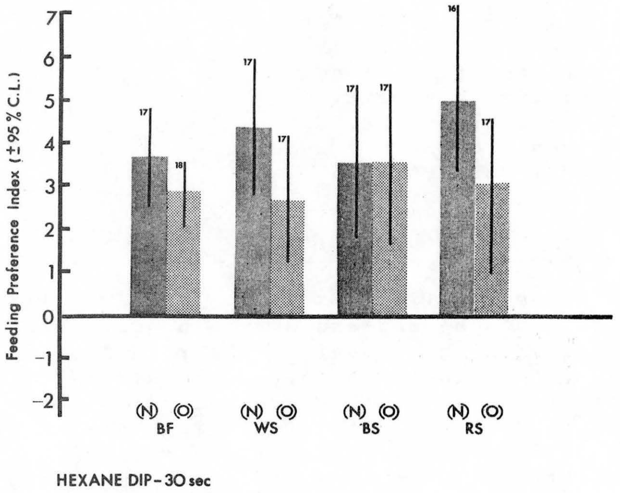
Figure 2 shows the Preference Index values for each host. In general, greater feeding occurs on discs treated with epicuticular waxes from the current year's growth from all hosts except black spruce where new and old needle waxes produce the same results. Red spruce shows the highest Preference Index followed by white spruce, then balsam fir and black spruce. The most significant finding for these tests is that the epicuticular waxes from all hosts, for both old and new needles, not only induce biting by larvae, but they also contribute to the maintenance of feeding though at a reduced level compared to sugars and glycosides (Albert, 1983; Fig. 2).

FIGURE 2. Feeding preference index for animals in two-choice tests using hexane extracts from new or old foliage from four host plants.

BF : Balsam fir
WS : White spruce
BS : Black spruce
RS : Red spruce

(N) : Current year's growth
(O) : 2-year-old growth

Numbers above histograms are the numbers of experimental animals. See Materials and Methods for definition of preference index.



A preliminary separation of the epicuticular waxes from balsam fir and white spruce current year's foliage was performed using gas chromatography and mass spectrometry techniques by Dr. A.P. Tulloch (Prairie Regional Lab, N.R.C., Saskatoon). The weights of purified materials recovered for each host are presented in Table 1. To date, the first three fractions from balsam fir have been tested, and each shows strong feeding stimulant activity. These contain hydrocarbons as well as esters.

Since pure fatty acids contained in the epicuticular wax from balsam fir are known (Beri and Lemon, 1970), we tested these at a concentration of 10^{-3}M. The results are shown in Table 2. Lauric, myristic, oleic, linoleic, linolenic, lignoceric, and palmitoleic acids all stimulate feeding. To test whether these could synergize with sucrose, a known polar feeding stimulant, tests with fatty acid and sucrose combinations were performed. Results are shown in Table 3. Myristic, oleic, and palmitoleic acids all enhance the feeding response to sucrose alone, with oleic acid having the greatest effect.

Some fatty acids which were not stimulating by themselves were also tested in combination with sucrose. Palmitic and heptadecanoic acids were shown to also increase the feeding response to sucrose (Table 4).

TABLE I. CHEMICAL FRACTIONS RECOVERED FROM EPICUTICULAR WAXES OF BALSAM FIR AND WHITE SPRUCE, HEXANE DIP, 30 SEC, CURRENT YEAR NEEDLES.

Balsam fir.
Sample weight: 0.340 g

No.	Weight	Comments on composition
1	0.0113	Hydrocarbons (considerably contaminated)
3	0.0500	Methyl esters C_{22}-C_{34}; Esters of hexanol (and octanol) C_{32}-C_{44}. Numerous unidentified components but no aldehydes detected (difference from white spruce)
4	0.0720	Mostly di(2-ethylhexyl) phthalate (contaminant) and some esters
5	0.0110	Phthalate ?
7	0.0450	10-nonacosanol
8	0.0460	Some free acids C_{22}-C_{30} and small amount of C_{32}-C_{36} triacyl glycerols
9	0.0210	Small free alcohols C_{18}-C_{30}
10	0.0700	
11	0.0800	Small diols (C_{29} like those in Juniper wax)

Fractions 8 to 11 also contain numerous unidentified components, possibly diterpene acids and probably appreciable amounts of polyesters (estolides) which are always found in conifer waxes.

White spruce.
Sample weight: 0.196 g

No.	Weight	Comments on composition
1	0.0060	Hydrocarbons (considerably contaminated)
3	0.0210	Methyl esters C_{22}-C_{32}. Esters of hexanol and octanol C_{36}-C_{42}. Aldehydes C_{22}-C_{32}. Numerous unidentified components
4	0.0080	Phthalate ?
5	0.0050	
6	0.0120	
7	0.0450	10-nonacosanol
9	0.0110	Free acids C_{22}-C_{32}
10	0.0730	Acids C_{16}-C_{30}. Alkanols C_{22}-C_{28}. Diols

See footnote to balsam fir composition.

Data compliments of Dr. A.P. Tulloch, NRC Prairie Regional Lab, Saskatoon, Saskatchewan. GC-Mass Spec. separations.

TABLE 2. MEAN % CONSUMPTION OF DISCS TREATED WITH WATER (CONTROL) AND WITH FATTY ACIDS IN TWO-CHOICE TESTS

MEAN % CONSUMPTION (±S.E.)				
CONTROL (H_2O)	FATTY ACID (10^{-3}M)		N	P
58.5 (3.7)	41.5 (3.7)	CAPRIC	17	0.026
33.7 (3.7)	66.3 (3.7)	LAURIC	14	0.002
36.4 (2.9)	63.6 (2.9)	MYRISTIC	18	0
54.2 (5.0)	45.8 (5.0)	PENTADECANOIC	14	0.510
58.4 (4.6)	41.6 (4.6)	PALMITIC	15	0.045
56.6 (5.4)	43.4 (5.4)	STEARIC	17	0.266
34.7 (2.8)	65.3 (2.8)	OLEIC	17	0.001
41.4 (3.0)	58.6 (3.0)	LINOLEIC	18	0.019
38.6 (3.6)	61.4 (3.6)	LINOLENIC	17	0.015
46.3 (2.9)	53.7 (2.9)	ARACHIDIC	16	0.211
48.7 (3.4)	51.3 (3.4)	BEHENIC	18	0.542
35.4 (3.5)	64.6 (3.5)	LIGNOCERIC	18	0.002
35.6 (3.0)	64.4 (3.0)	PALMITOLEIC	17	0.002
44.7 (3.8)	55.3 (3.8)	HEPTADECANOIC	18	0.136

N= Number of experimental animals

P= probability values, Wilcoxon's Signed-Ranks Test

TABLE 3. MEAN % CONSUMPTION OF DISCS TREATED WITH SUCROSE (0.025M) AND WITH A COMBINATION OF SUCROSE AND FATTY ACID IN TWO-CHOICE TESTS

MEAN % CONSUMPTION (±S.E.)				
CONTROL SUCROSE (0.025M)	0.025M SUCROSE +FATTY ACID (10^{-3}M)		N	P
45.1 (2.6)	54.9 (2.6)	LAURIC	19	0.084
38.8 (2.7)	61.2 (2.7)	MYRISTIC	20	0.002
32.4 (3.0)	67.6 (3.0)	OLEIC	16	0.001
48.6 (2.3)	51.4 (2.3)	LINOLEIC	17	0.813
46.7 (2.6)	53.3 (2.6)	LINOLENIC	18	0.246
46.5 (3.2)	53.5 (3.2)	LIGNOCERIC	16	0.281
40.8 (3.1)	59.2 (3.1)	PALMITOLEIC	18	0.012

N= Number of experimental animals

P= probability values, Wilcoxon's Signed-Ranks Test

TABLE 4. MEAN % CONSUMPTION OF DISCS TREATED WITH SUCROSE (0.025M) AND WITH A COMBINATION OF SUCROSE AND A FATTY ACID IN TWO-CHOICE TESTS

MEAN % CONSUMPTION (±S E.)				
CONTROL SUCROSE (0.025M)	0.025M SUCROSE +FATTY ACID (10^{-3}M)		N	P
47.9 (3.9)	52.1 (3.9)	CAPRIC	16	0.638
42.7 (3.2)	57.3 (3.2)	PENTADECANOIC	14	0.056
41.3 (2.6)	58.7 (2.6)	PALMITIC	20	0.002
46.9 (2.9)	53.1 (2.9)	ARACHIDIC	19	0.420
55.2 (3.2)	44.8 (3.2)	BEHENIC	17	0.136
39.9 (3.5)	60.1 (3.5)	HEPTADECANOIC	16	0.005

N= Number of experimental animals

P= probability values, Wilcoxon's Signed-Ranks Test

Epicuticular waxes are obviously of some importance in the feeding behavior of eastern spruce budworm larvae. They are the first gustatory chemicals which the insect encounters while palpating the surface of the leaf prior to biting and feeding. It is reasonable to assume that some of the chemicals serve to trigger the "test bite" response. However, their role may be much more important in serving to enhance the feeding response to the polar and non-polar compounds present within the leaf sap. The exact nature of this effect remains to be examined in greater detail both by behavioral and by electrophysiological techniques. More importantly, a study of the effects of epicuticular waxes on the feeding behavior of second- and third-instar larvae may shed some light on their possible role in stimulating these early instars to establish feeding sites on the developing buds. It is at this stage that a feeding or biting deterrent would likely be most effective in preventing larvae from establishing themselves on a host plant.

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THE QUEST FOR ANTIFEEDANTS FOR THE SPRUCE BUDWORM (CHORISTONEURA FUMIFERANA (CLEM.)

M.D. Bentley

Professor of Chemistry, University of Maine,
Orono, ME. 04473

D.E. Leonard

Professor of Entomology, University of
Massachusetts, Amherst, MA. 01002

G.M. Strunz[1]

Research Scientist, Maritimes Forest Research
Centre, Canadian Forestry Service, Fredericton,
N.B., Canada. E3B 5P7

Extracts of non-host plants and selected naturally occurring compounds have been screened for their effects on feeding by spruce budworm larvae, (Choristoneura fumiferana (Clem.), using as diet a filter paper substrate impregnated with the synergistic feeding stimulants, sucrose, and L-proline. The most potent feeding deterrents identified to date are alkaloids.

A simple, fast and reproducible feeding assay for spruce budworm larvae, (Choristoneura fumiferana (Clem.), was described by Bentley, Leonard, and Mott (1979).

For the assay, sixth-instar larvae are induced to feed on a filter paper substrate impregnated with the synergistic feeding stimulants sucrose and L-proline. Frass resulting from ingestion of this material is readily recognizable, and counts of frass pellets provide an indication of the quantity consumed. The effects on feeding of adding plant extracts and test chemicals to the substrate can thus be investigated readily. Its simplicity, speed, and modest requirements for test material make this assay suitable for mass screening, and it has, to date, been used to test more than 110 non-host plants, as well as about 60 naturally occurring chemicals, for their effects on budworm feeding.

An analysis of the results, published recently (Bentley et al. 1982), reveals that although none of the plants tested is a normal host of spruce budworm larvae, only six extracts displayed activity in the category designated "highly deterrent". All plants belonging to the most active group are known to contain alkaloids, and, in each case, the greatest activity was found to be localized in the basic fractions. Among the pure alkaloids tested, including representatives of the pyrrolizidene, solanum, quinolizidine, berberine, and strychnos groups, fewer than 25% were "highly deterrent" at the concentrations assayed.

Recent research has been directed to a "fine-tuning" of the bioassay, to provide greater sensitivity and allow more protracted observation of the effects on larvae of the test compounds. In addition, further screening is planned in an attempt to identify potent feeding deterrents with minimal toxic properties. A study of the structure-activity relationships which have begun to emerge may prove to be a profitable direction for future research.

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FOLIAGE CONSUMPTION BY 6TH-INSTAR SPRUCE BUDWORM LARVAE, *CHORISTONEURA FUMIFERANA* (CLEM.), FEEDING ON BALSAM FIR AND WHITE SPRUCE

A.W. Thomas

Research Scientist
Maritimes Forest Research Centre
Canadian Forestry Service
Fredericton, New Brunswick, Canada E3B 5P7

Female larvae ate about 1.5 times as much foliage as male larvae. Larvae ate significantly less old foliage than current foliage. Balsam fir current foliage was eaten in greater quantitities than any other foliage; white spruce current and balsam fir old were eaten to the same extent; very little old white spruce was eaten.

Introduction

To model the effect of budworm larval density on loss of fibre production in balsam fir and white spruce, data on the amount of current and old foliage consumed by larvae are required. This paper summarizes the work, to date, on the continuing study.

Materials and Methods

Field-collected branches of each host species were trimmed to the current year's growth attached to the apical 4 cm of the previous year's growth from which all needles had been removed. Other shoots were trimmed to 1-yr-old foliage attached to 4 cm of the previous year's growth. About 250 such shoots were prepared from any one tree at any one time. Each shoot was placed in water overnight. The following day, surface water was removed from the stem and the shoot was weighed. Shoots that had wilted overnight were discarded. Each shoot was placed in a numbered screen-topped cup with the base of the shoot projecting through a hole in the bottom of the cup and into water. One newly-moulted, i.e., less than 8 h old, unfed 6th-instar larva was placed in each cup with one shoot. Approximately 100 males and 100 females were used for each experiment. The remaining 50 shoots were used to construct a standard curve relating foliage dry weight to fresh weight. These shoots were oven-dried at 65°C when 50% of the larvae had pupated. The standard curve was used for predictive purposes.

The experiments were carried out in a room at 26°C, 80% RH, and a 16 h photoperiod. As each larva pupated, the pupa was placed in a glass vial and the shoot was oven-dried.

The dry weight of the shoot offered to each larva was predicted from a regression of dry weight on fresh weight, i.e., from the standard curve. The ovendry weight of the shoot at the end of the larval feeding period was subtracted from the predicted original dry weight. The difference in dry weights was an estimate of the amount eaten.

The frass produced by each 6th-instar larva was oven-dried and weighed. After 24 h, emerged moths were killed, oven-dried, and weighed.

Results and Discussion

Standard Curves

The correlation coefficient between dry weight and fresh weight of foliage was very high for both current and old foliage; 10 standard curves for balsam fir ranged between 0.903 and 0.997 and averaged 0.977; 6 curves for white spruce ranged between 0.972 and 0.999, averaging 0.990. However, the standard errors and consequently the 95% prediction limits about the mean of a new sample were too high for the dry weight of a single shoot, or even small samples, to be predicted with sufficient accuracy. For example, the standard errors, for different sample sizes, of predicted mean dry weight for balsam fir current year foliage having a mean fresh weight of 3.64 g were obtained from the following regression

Dry weight (mg) = 31.06 + 308.41 fresh weight (g)
$r = 0.99$, $n = 51$, $Sy.x = 4683.9$

Sample size	Standard error, mg
5	32.6
10	24.4
20	19.0
40	15.7
80	13.7

Because the proportion of water present in current year shoots drops continuously during the growing season, a standard curve had to be developed for each experiment. When 6th-instar larvae first appear in the field, the water content of the current year shoots is 80-85%, by the end of the growing season it is 55%, and in 1-yr-old foliage water content is 49%.

Foliage Consumption

The data from four experiments using balsam fir current year foliage were pooled, and similar data from four experiments using balsam fir old foliage were pooled. The average amount of current foliage consumed by a 6th-instar female larva ($n = 203$) was 315 mg dry weight, for males it was 207 mg ($n = 174$). For old foliage the average figures were 201 mg ($n = 95$ females) and 128 mg ($n = 139$ males). This reduction in consumption associated with old foliage affected both males and females to the same extent, about 38%. Females ate 1.52 as much current foliage and 1.57 as much old foliage as did males.

The above statistics refer to larvae that eventually emerged as moths. During the study, some pupae died. Females that died in the pupal stage consumed an average of only 211 mg of current fir foliage whilst males consumed an average of 132 mg.

The data from three experiments using white spruce current year foliage were pooled, and similar data from four experiments using white spruce old foliage were pooled. The average amount of current foliage consumed by a 6th-instar female larva (n = 152) was 190 mg dry weight, for males it was 134 mg (n = 122). For old foliage the average figures were 92 mg (n = 108 females) and 67 mg (n = 83 males). As with balsam fir, the reduction in consumption associated with old white spruce affected both males and females to the same extent. However, this reduction in consumption of white spruce, 51%, was greater than the 38% reduction associated with old fir. Females ate 1.42 as much white spruce current foliage and 1.37 as much old foliage as did males.

Females dying as pupae ate, on average, 156 mg of white spruce current foliage whilst males ate 125 mg.

Both male and female 6th-instar larvae eat significantly more balsam fir than white spruce, a difference that holds true for both current and old foliage. As white spruce produces more foliage than balsam fir, the net effect is less defoliation on white spruce, and presumably less fibre loss, if there is approximately the same density of larvae on each tree.

Tree Species and Insect "Performance"

The dry weight of a 24-h-old moth is a convenient measure of an insect's performance. White spruce current year foliage produced the largest moths, males averaged 11.6 mg, females averaged 21.1 mg; followed by balsam fir current year foliage, males 8.2 mg, females 15.3 mg. Balsam fir old foliage produced males which averaged 7.3 mg and females which averaged 11.6 mg. White spruce old foliage gave rise to very small moths; males averaged 2.9 mg and females averaged 4.7 mg.

White spruce current foliage also proved to be the most efficient diet in the sense that the ratio, dry weight of needles eaten:dry weight of moth, was lower than for any other foliage, i.e., 12:1 for males, 9:1 for females. The other foliages were relatively inefficient. Balsam fir old foliage although producing smaller moths than balsam fir current foliage was the next most favorable diet in that the ratios for both males and females were 17:1. Balsam fir current foliage had a ratio of 25:1 for males and 21:1 for females. White spruce old foliage ratios were 23:1 for males and 20:1 for females.

Because of the problem, with this method, of obtaining sufficient accuracy of the amount eaten, I have been able to deal only with means. For a better understanding of the system it is preferable to use data from individual insects, or trends. An indirect way of looking at consumption is to consider frass production. This has the distinct advantage that the amount of frass produced can be measured without error. It is also reasonable to assume that frass production is representative of the amount eaten. Thus, another way of comparing insect performance on the two hosts is to compare the relationship between moth weight and frass produced by 6th-instar larvae.

Dry frass weight and dry moth weight were correlated and regressions, for comparative purposes, could be defined. For young current shoots of white spruce, collected 31 May 1982, containing 83% water, the regression of frass produced by 6th-instar female larvae on subsequent moth dry weight was

Frass (mg) = 39.37 + 5.010 moth weight (mg)
r = 0.82, n = 101, Sy.x = 401.79

For similar shoots from the same tree, but collected 15 days later, and containing 71% water, the regression was

Frass (mg) = 39.09 + 8.965 moth weight (mg)
r = 0.79, n = 17, Sy.x = 114.43

Young current white spruce was the preferred diet in that it produced a moth of a given weight more efficiently than slightly older current foliage, e.g., a female of dry weight 15 mg would have produced 114 mg of frass as a 6th-instar larva feeding on young current shoots, but two weeks later would have produced 174 mg of frass. On average, the ratio of frass weight:moth weight was 6.8:1 for young current foliage and 13.1:1 for older current foliage. A similar trend was seen with males and for both sexes feeding on young and older current year balsam fir needles.

These data confirm the earlier conclusion that current foliage is a preferred diet and they also suggest that such foliage rapidly looses quality. The scenario envisaged for white spruce is that the youngest foliage of the current year is the preferred food, relatively small amounts are required to produce a moth of a certain size; as the foliage ages its suitability as a food declines, it is still readily palatable but more of it is required to produce a moth of a certain size; as it ages still further, it becomes unpalatable and larvae eat very little of it.

WESTERN SPRUCE BUDWORM CONSUMPTION - EFFECTS OF HOST SPECIES AND FOLIAGE CHEMISTRY

Michael R. Wagner and Elizabeth A. Blake

Assistant Professor and Graduate Research Assistant
School of Forestry, Box 4098
Northern Arizona University
Flagstaff, AZ 86011

Feeding efficiencies and growth rates of western spruce budworm larvae varied among hosts tested. Pupae attained normal size regardless of host species. Candidate defensive compounds (tannins and phenols) varied only slightly with the vigor of the host. The relationship between these defensive compounds and measures of larvae growth were not entirely consistent with current theories on the role of secondary plant compounds.

Introduction

Within a population of host plants, the intensity of insect attack and subsequent damage may vary considerably. It is not uncommon for two Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, trees near each other to have quite different populations of western spruce budworm, *Choristoneura occidentalis* Freeman (McDonald 1981). Western spruce budworm (WSBW) frequently exhibits this preferential habit within and among its hosts in the Southwest.

Numerous explanations for preferential attack by insects have been suggested including differences in nutritional values, phenology, foliage toughness, host vigor, and plant defensive compounds. Foliage chemicals have been implicated as specific factors in the resistance-susceptibility characteristics of Douglas-fir (McMurray 1980). Literature on the important plant defensive compounds has been adequately reviewed by the following authors: tannins (Swain 1979), phenols (Levin 1971, Swain 1977), and nitrogen (Mattson 1980).

In this paper we present some preliminary results on differences in feeding by WSBW among the important hosts in the Southwest. We also report on correlations between WSBW feeding and concentrations of phenols, tannins, and proteins in white fir, *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., and Douglas-fir foliage.

Methods

Tree Selection

Four hosts of WSBW occurring in northern Arizona were selected for the feeding experiments: Douglas-fir, white fir, corkbark fir, *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.; and Engelmann spruce, *Picea engelmannii* Parry ex Engelm. Trees were selected from mixed conifer stands approximately 16 km north of Flagstaff, Arizona, stand elevation approximately 2,440 meters. These stands had no recent history of WSBW outbreaks.

Trees suitable for site index determination were rated for vigor according to Waring et al. (1980). This technique uses the ratios of the basal area growth for one-year and five-year increments to total sapwood area. To obtain average measurements, four increment cores were taken at 90° angles from each of 25 trees of each host species. The increment cores were then stained with potassium iodide-iodine to aid in distinguishing the sapwood from the heartwood (Kutscha and Sachs 1962). Total radius, sapwood radius, and one- and five-year increment radii were measured. The ratios were calculated using this formula:

$$\frac{BA_x}{SA} = \frac{R^2\pi - (R - r_x)^2\pi}{R^2\pi - (R - r_s)^2\pi}$$

BA_x: basal area of growth increment for period x

SA : sapwood area

R : total radius

r_x : radius of increment growth

r_s : radius of sapwood

Fifteen trees were selected from the 25 which were cored for each species (five trees in each of three vigor categories). The five trees with the highest ratios were classified as high vigor trees, the five trees with the lowest ratios were classified as low vigor trees, and the five trees closest to the mean were classified as medium vigor trees. The theoretical range of BA/SA ratio is 1.00 to 0.00. The actual range of BA_5/SA observed for the four species was: Douglas-fir 0.49 to 0.14, white fir 0.59 to 0.20, corkbark fir 0.63 to 0.24, and Engelmann spruce 0.60 to 0.13.

Selection of Larvae

Second and third instar larvae were collected in early May from an ongoing WSBW outbreak within the Kaibab Naitonal Forest, Arizona. Budworm infested branch tips were collected from the four host species used in this study. Larvae were carefully segregated according to host species; this allowed the larvae to be fed foliage from the same host species from which they were collected. The branch tips were placed in Aquapics® to maintain freshness and transported to the laboratory.

The field collected larvae were stored at 2-4°C to slow development until five to seven days before the experiments were to begin. The larvae were then placed at room temperature until they advanced to the fourth instar. Larvae were determined to be in the fourth stadium by head capsule measurements. Bean and Blatzer (1957) and Wagg (1958) were used as guidelines.

Foliage Collection

To standardize the host phenological stage, feeding experiments were begun when the host foliage was determined to be at the "brush" stage (bud cap gone, needles even but no shoot growth so needles appear to arise from one spot) (Shepard unpublished).

We collected paired foliage samples from the midcrown of the host trees at the four cardinal directions. Paired twigs were selected for uniformity in size and phenology. One twig was fed to a budworm, the other twig was used to estimate the average dry weight per needle of the feeding twig. This average dry weight was later used to estimate the dry weight of the foliage consumed by the budworm larva.

Feeding Procedure

The paired twigs were saturated in a 100% relative humidity environment overnight. The following morning the mature foliage was trimmed from the feeding twig. While being held under water, the twig was excised and placed in a water-filled Aquapic®. The prepared foliage was then placed in a paper-lined 150 x 25 mm petri dish.

Fourth instar larvae were weighed fresh and placed on the prepared foliage to feed. Initial dry weight of each larva was estimated using an average percent dry weight of fourth instar larvae. The petri dishes were placed in controlled environmental chambers for the duration of the experiments. Temperature in the chambers ranged from 24 to 26°C; the photoperiod was 16 hours of light and 8 hours of darkness, as recommended by Robertson (1979).

Following each 72 hour feeding period the feeding twigs were removed and replaced with fresh foliage. The number of damaged needles was recorded and the damaged needles still attached to the twig and wasted needles were collected and oven dried at 60°C until no further weight loss occurred. Both wasted and remaining foliage were then weighed on a balance accurate to 0.1 mg. The amount of foliage ingested by each larva was estimated using the following formula:

$$I = (DW \times N) - (W + R)$$

I : foliage ingested

DW: mean dry weight per needle

N : number of needles damaged

W : foliage wasted (clipped but not consumed)

R : foliage remains (damaged but not clipped from the twig)

Each replicate was terminated within 24 hours of pupation. Total foliage ingested was calculated; pupae were sexed and weighed fresh. Feces and pupae were then oven dried at 60°C and weighed.

Nutritional indices were calculated on a dry weight basis according to Waldbauer (1968). The following nutritional indices are used in this study: foliage ingested (I), relative consumption rate (RCR), relative growth rate (RGR), approximate digestibility (AD), and efficiency of conversion of ingested food to body weight (ECI).

Chemical Analysis

Foliage used in the chemical analyses was clipped from the host trees selected for the feeding experiment and immediately frozen for 18 hours at -20°C. Samples were then freeze-dried at -50°C and 50 millitorr in a freeze dryer. Samples were stored at -20°C under dessication until analyzed.

Proteins were analyzed using the Coomassie Brilliant Blue Dye technique (Bradford 1976). Total phenols were determined using the Folin-Denis technique according to Swain and Hillis (1959) and Ribereau-Gayon (1972). Tannins were analyzed using the vanillin reaction assay (Price et al. 1978) as modified by Zucker (unpublished).

Results and Discussion

Comparison of Rearing Methods

The effect of three commonly used rearing procedures on fresh and dry pupal weights was determined for WSBW feeding on Douglas-fir and corkbark fir. Fresh pupal weights were significantly different among rearing methods for corkbark fir but not for Douglas-fir (Table 1). For corkbark fir, fresh pupal weights were significantly higher for insects bagged on foliage in the field than for insects fed excised foliage in the lab. Excised foliage and bagged foliage tests were conducted on the same trees and crown positions. Fresh pupal weights were not significantly different between insects reared on excised foliage and insects that developed under normal field conditions for either host species. Dry weights of pupae were not significantly different between rearing methods (Table 2).

Table 1. Fresh pupal weights of female western spruce budworm by rearing method and host species. a/

REARING METHOD	DOUGLAS-FIR	CORKBARK FIR
EXCISED FOLIAGE	70.6 (5)[b]	69.0 (5) A[c]
FIELD BAGGED	91.6 (4)	83.6 (6) B
FIELD COLLECTED	70.5 (77)	59.8 (51) A
F-PROB.	0.1390	0.0014

a/ weights in milligrams.
b/ numbers in parentheses are number of cases.
c/ oneway ANOVA, LSD multiple range test, $\alpha = 0.10$, values followed by different letters are significantly different.

Table 2. Oven-dry pupal weights of female western spruce budworm by rearing method and host species. a/

REARING METHOD	DOUGLAS-FIR	CORKBARK FIR
EXCISED FOLIAGE	20.8 (5)[b]	19.2 (5)
FIELD BAGGED	16.4 (4)	18.7 (6)
FIELD COLLECTED	———	———
F-PROB.	0.4705	0.8974

a/ oneway ANOVA, $\alpha = 0.10$, LSD multiple range test, values followed by different letters are significantly different.
b/ numbers in parentheses are number of cases.

The technique of excising foliage for feeding experiments may lead to misleading results if inducible defensive mechanisms exist, because excised branches may not be able to respond to insect feeding by increasing concentrations of defensive compounds as would a normal branch. However, our study shows that feeding on excised foliage in the laboratory is probably a good approximation of feeding as it occurs under natural conditions. Bagging of insects on trees (white muslin bags) tends to increase pupal weights, probably as a result of reduced harassment from predators and parasites and possibly because of a modified microclimate.

Influence of Host Species

A commonly held belief among foresters is that some host species are more resistant to both WSBW and eastern spruce budworm, *Choristoneura fumiferana* Clemens, than are other hosts. We compared the relative suitability of three of the important hosts in Arizona (Table 3). Pupal weights were not significantly different among the three hosts, which indicates that all hosts are a suitable substrate for insect development. Feeding efficiency (ECI) and growth rate (RGR) were significantly higher on Douglas-fir than on either white fir or corkbark fir. However, budworm larvae can apparently compensate for the lower quality of the foliage, as reflected in low ECI and RGR, by increasing their consumption rate (I) and probably the duration of the feeding period. This ability of insects to compensate for lower food quality by increasing consumption is often overlooked in studies of host plant-herbivore interaction. Too few replicates of Engelmann spruce were available to include in this analysis; however, qualitatively it appeared as if WSBW did quite well on spruce foliage when the host growth and the herbivore requirements were synchronized.

Table 3. Nutritional indices and pupal weights for western spruce budworm reared on three host species in Arizona.

HOST	N	I (mg)	RCR	RGR	ECI	PUPAL WT.[a] (mg)
DOUGLAS-FIR	13	185.	1.7	0.12 A[b]	7.8 A	58.6
WHITE FIR	20	226.	2.0	0.10 B	5.4 B	60.6
CORKBARK FIR	10	223.	1.7	0.09 B	5.8 B	60.0
F-PROB.		0.341	0.163	0.012	0.003	0.957

a/ pupal weight on fresh basis, all other values based on oven-dry weights.
b/ values followed by different letters are statistically significant, oneway ANOVA, LSD multiple range test, $\alpha = 0.10$.

Chemical Content of WSBW Host Foliage

Current year's foliage of selected host trees was collected seven to 10 days after the beginning of the feeding studies. Foliage was collected from the same trees and crown position as those used in the feeding studies. Tannin concentration did not vary significantly between host vigor categories for any of the species tested (Table 4). Engelmann spruce had approximately twice the tannin content of any other host. Total phenols were not different among vigor categories for Douglas-fir and white fir (Table 5). However, medium vigor corkbark fir trees had lower total phenols than did the high or low vigor trees. Low vigor Engelmann spruce trees had lower total phenols than high and medium vigor trees. Protein content of foliage tended to decrease with host vigor for all host species tested (Table 6). However, this trend was statistically significant only for Engelmann spruce.

Table 4. Percent dry weight of tannins in western spruce budworm host foliage by host vigor class. a/

VIGOR	DOUGLAS FIR		WHITE FIR		CORKBARK FIR		ENGELMANN SPRUCE	
HIGH	4.78	A	5.64	A	4.51	A	9.12	A
MEDIUM	3.91	A	4.58	A	4.98	A	9.71	A
LOW	4.98	A	3.79	A	4.40	A	8.86	A
$\bar{x}$	4.49		4.66		4.63		9.28	

a/ values followed by different letters are significantly different, oneway ANOVA, LSD multiple range test, $\alpha = 0.05$.

Table 5. Total phenol content of western spruce budworm host foliage by host vigor class. a/ b/

VIGOR	DOUGLAS FIR		WHITE FIR		CORKBARK FIR		ENGELMANN SPRUCE	
HIGH	0.11	A	0.07	A	0.19	A	0.12	A
MEDIUM	0.10	A	0.06	A	0.13	B	0.13	A
LOW	0.09	A	0.06	A	0.18	A	0.08	B
$\bar{x}$	0.10		0.06		0.17		0.11	

a/ total phenols expressed in terms of absorbance per mg.
b/ values followed by different letters are significantly different, oneway ANOVA, LSD multiple range test, $\alpha = 0.05$.

Table 6. Percent dry weight of protein in western spruce budworm host foliage by host vigor class. a/

VIGOR	DOUGLAS FIR		WHITE FIR		CORKBARK FIR		ENGELMANN SPRUCE	
HIGH	14.62	A	21.17	A	22.78	A	23.88	A
MEDIUM	12.41	A	20.85	A	19.08	A	22.90	A
LOW	11.69	A	17.47	A	19.86	A	16.77	B
$\bar{x}$	12.86		19.93		20.57		21.36	

a/ values followed by different letters are significantly different, oneway ANOVA, LSD multiple range test, $\alpha = 0.05$.

Relationship Between Foliage Chemistry and Insect Feeding

Pearson's correlation coefficients and a simple linear regression were used to evaluate the relationship between foliage chemistry and WSBW feeding. In each case foliage samples for chemical analysis and feeding were collected from the same aspect and crown position of the same tree. Only Douglas-fir and white fir are discussed here due to insufficient sample size for the other species.

Tannins in Douglas-fir were positively correlated with both foliage ingested and approximate digestibility (Table 7). These results were quite surprising considering that the theory of plant apparency (Feeny 1976, Rhoades and Cates 1976) would predict that the quality of the foliage and subsequent consumption should decrease as tannins increase. Phenols are not significantly correlated with any of the larval growth parameters studied. Protein is positively correlated with pupal weight. Adjusted R^2 values presented in Table 8 indicate that leaf tannin content can be used to predict the amount of Douglas-fir foliage ingested and that protein content is a useful predictor of pupal weight.

Table 7. Correlation coefficients indicating the relationship between Douglas-fir foliage chemistry and western spruce budworm larval growth parameters (n = 7).

	LARVAL GROWTH PARAMETERS					
FOLIAGE CHEMICALS	INGESTED	RCR	RGR	AD	ECI	PUPAL WT.
TANNINS	0.72 a/	0.55	0.62	0.78 b/	-0.25	0.65
PHENOLS	0.26	-0.24	-0.37	-0.46	0.08	-0.38
PROTEINS	0.64	0.01	0.62	0.41	0.26	0.70 a/

a/ $P \leq 0.10$.
b/ $P \leq 0.05$.

The relationships between foliage chemicals and larval growth parameters for white fir are different from those observed for Douglas-fir. In this case tannins are negatively correlated with growth rate and efficiency (Table 9). This is consistent with the plant apparency theory. Adjusted R^2 values indicate foliage tannin content can be used to predict growth rate and efficiency (Table 10). Neither phenols nor proteins are correlated with any measure of larval growth for WSBW feeding on white fir foliage.

Table 8. Adjusted R^2 values for simple regression equations using Douglas-fir foliage chemicals to predict western spruce budworm larval growth (n = 7). d/

FOLIAGE CHEMICALS (x)	LARVAL GROWTH PARAMETERS (Y)					
	INGESTED	RCR	RGR	AD	ECI	PUPAL WT.
TANNINS	0.40[a]	NS[c]	NS	NS	NS	NS
PHENOLS	NS	NS	NS	NS	NS	NS
PROTEINS	NS	NS	NS	NS	NS	0.57[b]

a/ $P \leq 0.10$.
b/ $P \leq 0.05$.
c/ NS; not significant.
d/ data transformed where appropriate to best fit the form of the relationship.

Table 9. Correlation coefficients indicating the relationship between white fir foliage chemistry and western spruce budworm larval growth parameters (n = 8).

FOLIAGE CHEMICALS	LARVAL GROWTH PARAMETERS					
	INGESTED	RCR	RGR	AD	ECI	PUPAL WT.
TANNINS	0.44	0.42	-0.68[a]	0.45	-0.85[b]	-0.22
PHENOLS	-0.28	-0.33	-0.38	-0.17	-0.37	-0.27
PROTEINS	0.18	0.14	0.15	0.12	0.13	0.25

a/ $P \leq 0.10$.
b/ $P \leq 0.05$.

Table 10. Adjusted R^2 values for simple regression equations using white fir foliage chemicals to predict western spruce budworm larval growth (n = 8). d/

FOLIAGE CHEMICALS (x)	LARVAL GROWTH PARAMETERS (Y)					
	INGESTED	RCR	RGR	AD	ECI	PUPAL WT.
TANNINS	NS[a]	NS	0.38[b]	NS	0.64[c]	NS
PHENOLS	NS	NS	NS	NS	NS	NS
PROTEINS	NS	NS	NS	NS	NS	NS

a/ NS; not significant.
b/ $P \leq 0.10$.
c/ $P \leq 0.05$.
d/ data transformed where appropriate to best fit the form of the relationship.

Douglas-fir, corkbark fir, white fir, and probably Engelmann spruce are all suitable host material for WSBW when current foliage flush is synchronized with the larval feeding period. Douglas-fir is of slightly better quality than the other species tested. However, because of the ability of the budworm to compensate for lower food quality by consuming more foliage, larvae can grow and develop quite well on lower foliage quality hosts. It is possible that white fir and corkbark fir could actually sustain more defoliation damage than Douglas-fir because their foliage is of lower quality. This is important to keep in mind when considering low foliage quality as a criterion for selecting resistant species or genotypes. In northern Arizona, Douglas-fir and true firs typically sustain more damage than Engelmann spruce, but this may be primarily because spruce is not phenologically synchronized with the feeding cycle of the WSBW.

There are suprisingly few differences in the tannins and phenols tested among vigor categories. Our study fails to show any evidence that high vigor trees maintain higher levels of defensive chemicals than do low vigor trees. Nor is there any evidence to suggest that by excising foliage, and presumably preventing induction of defensive compounds, insects can perform better than if they feed on a host which could actively defend itself. There may be differences in protein content between vigor categories, but even in the worst case (foliage with only 11% protein) there appears to be adequate protein to sustain insect development.

Differences in tannins, phenols, and proteins among species are more striking. Tannins are almost twice as abundant in Engelmann spruce as in the other species. But, considering the different relationship between tannins in white fir and Douglas-fir and feeding parameters, it is uncertain whether high tannin content has a negative or positive effect. There are differences in phenols between species but, here again, there is no apparent relationship to feeding parameters. Douglas-fir, which based on efficiency and growth rate of larvae is the best host, actually had the lowest average protein content of the host species tested.

Phenols do not appear to influence feeding by WSBW even though the phenolic content in budworm hosts is within the concentration range that has been reported to influence host selection by aphids (Zucker 1982).

The relationship between foliage tannins and some of the larval growth parameters is intriguing. It is likely that the tannins are not identical in Douglas-fir and white fir. But, the levels of tannins are well within the range found by Feeny and Bostock (1968) who argued that higher tannin content is equated with lower food quality. Bernays (1981) suggests that tannins may actually be used as a nutrient source by grasshoppers. In Douglas-fir, tannins were positively correlated with digestibility. In white fir, tannins were negatively correlated with growth and efficiency. It is difficult to explain these apparently opposite results, except that tannins and proteins are intercorrelated in Douglas-fir which may result in a random correlation. Clearly we know little about the role of foliage tannins in larval feeding and growth in the WSBW.

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SPRUCE BUDWORM (CHORISTONEURA FUMIFERANA) PERFORMANCE IN RELATION TO FOLIAR CHEMISTRY OF ITS HOST PLANTS

William John Mattson

Principal Insect Ecologist
U.S. Department of Agriculture, Forest Service
North Central Forest Experiment Station
202 Pesticide Research Center
Michigan State University
East Lansing, MI 48824

Scott S. Slocum and C. Noah Koller
Research Assistants
University of Minnesota
Department of Entomology
St. Paul, MN 55108

Spruce budworm growth was best on balsam fir, poorest on lowland black spruce, and intermediate on upland white and black spruce. Growth was consistently, positively linked to foliar N and negatively linked to Fe, K, and select terpenes. Survival rates were not strongly, nor consistently linked to any of the measured foliar chemical traits.

The population dynamics of the spruce budworm, *Choristoneura fumiferana*, is clearly an ecosystem/biome level process. The process has many parts, all of which interact to some degree, and none of which is really well understood individually, not to mention how they operate together. The process starts, as we see it, by a budworm larva taking a bite out of a plant. The plant has a complex array of nutritive and nonnutritive chemicals that together affect budworm behavior, metabolism and ultimately growth, reproduction and/or death. Our primary objective has been to examine variations in budworm performance among different host tree species in relation to the foliar chemistry of these trees. The ultimate goal is to identify the major host factors regulating budworm performance.

This paper reports on our preliminary analyses of the growth and survival of budworms in relation to total nitrogen, mineral elements, mono-terpenes, and phenolics in its diet on three tree species: balsam fir, *Abies balsamea*; white spruce, *Picea glauca*; and black spruce, *Picea mariana*.

This study was conducted in two locations, the main plot being about 20 miles south of International Falls, Minnesota, in Koochiching County, and the secondary plot about 15 miles west of Cloquet, Minnesota, in St. Louis County.

Methods

In 1981, we selected 122 trees for the purpose of monitoring the performance of larval budworms in relation to foliar chemistry of these trees. Among this set were 20 white spruce, 25 black spruce, and 58 balsam fir which were divided into four classes: 24 small (1-5 m), 16 medium (5-10 m), 8 large (10-15 m), and 10 stress. Nineteen of the medium/large category were selected at random for the purpose of studying both early and late season (i.e., late summer) budworm performance.

On each tree we selected five branches at midcrown level, approximately 70° apart so as to encircle the tree. Each branch was then enclosed with a 36" long fine-mesh cloth sleeve cage which served as an enclosure for 15 second-stage larvae placed therein. Larvae were obtained from the laboratory colony of the Insect Rearing Service of the Forest Pest Management Institute, Environment Canada, Canadian Forestry Service in Sault Ste. Marie, Ontario. Each branch contained at least 30 new shoots. Budworms were removed at the pupal stage and subsequent moths were collected in the laboratory and frozen within 24 hours after emergence in preparation for freeze-drying to constant weight.

We started the experiment in all cases after shoot elongation had begun (approximately 300 degree days, using 2.8°C as the threshold and March 1 as the beginning date). Budworms normally emerge from hibernacula at about 200 degree days in northern Minnesota (Bean and Wilson 1964) whereas in New Brunswick it may be closer to 100 (Cameron *et al.*, 1968). Our records indicate that balsam "bud break" occurred at about 238 DD in our main plot. In 1981, we placed larvae on black spruce about 1 month later (6/22/81) than on balsam and white spruce so as to avoid any possible adverse effects of the late phenology of black spruce. In 1982 all tree species received larvae at 300 DD. Furthermore, in 1981, we also placed second stage larvae on 19 medium/large balsam on July 24. This is about the time that budworm first stage larvae are normally preparing for overwintering.

Foliage chemistry was measured only once during the larval period, at approximately the commencement of the fifth larval stage. This was done because the fifth and sixth stages consume 90-95 percent of the total diet (Miller 1977, Retnakaran 1983). Foliage was gathered from all sides of the tree at midcrown, immediately stored in coolers on dry ice and then frozen at the laboratory until used for analysis. Except for terpene analyses, the foliage was separated from stems, then lyophilized and ground to pass through a 40-mesh screen on a Wiley mill. It was then stored dry in a glass container in the dark until analysis. Details of the various analyses can be obtained from the authors on request.

Because the field studies did not permit control of temperatures during larval development, temperature effects may be confounded with tree effects when comparing budworm performance on different plots and at different times. In all cases we know the daily maximum, minima, and mean temperatures for our experiments as well as the precipitation values. Once we understand the budworm's temperature-growth responses we will be able to remove possible temperature effects from host effects.

Table 1.--Mean adult female and male weights (mg dwt) reared on different hosts in 1981 and 1982

Host plant	1981 Mean	SD	1982 Mean	SD	1981 Mean	SD	1982 Mean	SD	n[a]
	Females		Females		Males		Males		
BFir stress	21.44	5.64	22.13	5.11	10.24	1.92	12.91	2.95	10
BFir lge	19.28	4.91	22.42	4.32	9.66	2.02	12.40	2.71	8
BFir med	20.42	3.90	20.65	5.74	9.76	1.76	11.99	3.44	16
BFir sml	17.83	3.99	18.78	4.43	9.33	1.69	10.87	2.38	24
WSpr lge	16.81	5.50	18.49	6.33	7.31	1.93	12.43	3.02	10
WSpr sml	15.00	6.05	16.17	6.21	8.20	2.81	9.26	2.93	10
BSpr upld	15.06	10.37	19.04	6.01	8.12	1.89	10.67	2.78	10/20[c]
BSpr lowld	8.32	3.38	11.10	3.56	4.92	1.42	6.73	1.79	15
BFir late	13.56	3.09	na[b]	na	7.41	1.78	na	na	18

[a] Number of trees in each species class.
[b] No data available.
[c] Ten trees in 1981, twenty in 1982.

Results

Differences Among Species

Budworms clearly attained the highest adult weights on balsam fir (18-22 mg dwt), followed by white spruce (15-18.5 mg) or upland black spruce (15-19 mg) and then lowland black spruce (8-11 mg) (Table 1). The pattern was consistent between years for both sexes. The fact that white spruce-reared budworms were smaller than those from fir is contrary to results from eastern North America where such spruce-reared budworms are usually about equal to (Blais 1957, Greenbank 1963) or significantly larger (Koller and Leonard 1982, and see T. Thomas in this proceedings) than those from balsam fir. The upland black spruce data agree with previous research which suggests that it produces slightly smaller insects than does balsam fir but not necessarily less than does white spruce (Blais 1957, Greenbank 1963).

Variability in female weights was about 50 percent greater on the spruces than on balsam fir as estimated by the coefficients of variation ($SD/\bar{x}$) (Table 1). This was the result of the fact that some spruce trees consistently produced very small insects ($\leq$ 11 mg) while others consistently produced large insects ($\geq$ 20 mg) similar to those on large balsam fir.

Generation survival rates (from second instars to the adult stage) in 1981 revealed that balsam fir was a superior host followed by white spruce and then black spruce (Table 2). The pattern changed in 1982, however, showing that white spruce and lowland black spruce were not different from balsam. Upland black spruce, however, again showed the lowest survival rates. We cannot explain differences in the survival patterns between years except to hypothesize that weather conditions may have been responsible. Mean daily temperatures were about 2.4°C higher during the larval period in 1981 than in 1982 (16.7° vs. 14.3°). Mean daily maxima averaged nearly the same (23.8° vs. 22.9°) in both years but daily minima were about 4°C higher in 1981 (9.5° vs. 5.7°).

Table 2.--Survival rates and proportion of females from different hosts in 1981 and 1982

Host plant	Survival rate 1981	Survival rate 1982	Proportion females 1981	Proportion females 1982
BFir stress	.290	.282	.48	.51
BFir md/lge	.305	.276	.55	.48
BFir sml	.330	.327	.54	.51
WSpr all	.232	.351	.53	.51
BSpr upld	.130	.179	.71*[a]	.45
BSpr lowld	.120	.275	.60*	.51
BFir late	.157	na	.53	na

[a] Significantly ($p \leq .05$) different from .50 ratio.

Differences Among Age Classes

We studied budworm performance on three age/size classes of trees (3-5 m, 5-10 m, 10-15 m) known as small(s), medium(m), and large(l), respectively. All trees were nearly open grown so most had full tree crowns. Large trees were bearing male flowers in the upper half crown level, whereas only few of the medium and none of the small trees were flowering.

In both balsam and white spruce, there was a consistent trend for small trees to produce the smallest insects. This pattern held between years and for both sexes. For example, the female mean dry weights (mg) for each size class shown in the following tabulation are significantly different ($p \leq .05$) from one another:

1981 BFir: 20.35(m) 19.26(l) 17.83(s)
1982 BFir: 22.42(l) 20.65(m) 18.78(s)
1981 WSpruce: 16.81(l) 15.09(s)
1982 WSpruce: 18.49(l) 16.17(s)

The smallest difference between mean female weights on small and the large-medium classes ranged from 1.4 to 1.9 mg on balsam and 1.7 to 2.3 mg on white spruce. The differences imply that insects growing on large-medium trees averaged at least 10 percent larger than those from small trees and in some cases as much as 20 percent. Survival rates, however, did not vary significantly among age classes (Table 2). Therefore, although small balsam and white spruce produced smaller insects, they did not produce lower survival rates than larger trees. In general, for both balsam and white spruce, mean insect weight gains and survival rates per tree had no correlation with one another.

Differences Owing to Phenology

On July 24, 1981, we "planted" second stage budworm larvae on 19 medium-large balsams. This date is nearly 2.5 months later than budworm second stage larvae normally emerge for feeding in northern Minnesota. The larvae on these trees attained only about two-thirds the size (13.56 mg) of normal early-season larvae (Table 1). Furthermore, survival was only about half (16%) of that experienced by the similar early-season cohort (Table 2). This was not unexpected because late summer foliage conditions are drastically different from those of early season. The fact that budworms performed as well as they did, however, was surprising. Mean daily temperatures during this late season experiment were about 2°C higher (18.9° vs. 16.7°) than during the early season experiments.

Differences Owing to Stress Treatments

Ten trees (7 medium and 3 large) were trenched at a radius of 10 feet from the trunk in the spring of 1980 down to depth of about 30 inches. This depth reached well into the mineral soil layer or hit bedrock since the study plot was on top of a rock outcrop covered with shallow soils. The ground area under each tree canopy was then covered with black polyethylene plastic. Trees were monitored for moisture stress by pressure bombing twigs that were collected near the bottom of the crown. Pressure bomb readings were taken once per week and two times per day (before 8:00 a.m. and after 2:00 p.m.), during the 6-week larval growth period. The following tabulation shows the mean seasonal pressure bomb differences (stress-control) at both a.m. and p.m. samples:

	a.m. difference	p.m. difference
1981	0.50 bars	0.89
1982	0.45 bars	0.78

Mean differences in water potential between stress and control trees were usually less than one bar--suggesting that the stress treatment was relatively weak. The differences were nevertheless statistically significant on half of the sample periods each summer.

Stress trees produced significantly larger female and male insects than the control trees (all medium and large firs combined) (Table 1). However, in 1982 only males were significantly larger than those from the control trees. The mean weight differences (stress-control) for each sex are shown in the following tabulation:

	Females	Males
1981 (Stress-Control):	1.31 mg	0.53
1982 (Stress-Control):	0.79 mg	0.80

Thus, so far, the induced stress treatment has had only a minor enhancing effect on budworm growth. However, it has not had any effect on survival rates (Table 2).

Budworm Performance in Relation to Foliar Nutrients

Theoretically an insect's performance should vary in relation to its dietary needs and a diet's deviations from these needs. In the case of the spruce budworm, no one really yet knows what the particular details of its needs are. Mattson and Koller (1981) proposed that the minimally optimal foliar N value for female performance is about 2.1 percent dwt. Harvey (1974) proposed that the minimally optimal levels of soluble sugars in the female's diet is about 4 percent fwt or 20 percent dwt. Albert *et al*, (1982) found that peak behavioral (*i.e.*, feeding) response to soluble sugars (sucrose) in the diet occurs at about .03M or less than 1 percent fwt. Thus diets deviating negatively from these values probably will produce smaller insects and/or longer growth and feeding periods. Requirements for other important dietary components are really unknown.

To obtain a perspective on the budworm's needs for the mineral elements, we analyzed the nutrient levels in the bodies of adult males and females collected from the trees in our study and then compared their body levels to their food levels (Table 3). The data reveal that the elemental concentrations showing highest deviations from foliar levels are as follows for males and females:

Females: Na>N>P>Cu>Zn>Fe>Mg>K>Ca>Mn
Males: Na>N>Cu>P>Zn>Fe>Mg>K>Ca>Mn

Sodium clearly had the highest magnification factor (MF) (60.9 and 13.4), but owing to possible errors in its measurement on our emission spectrometer we consider the results very tentative. Nitrogen, P, and Cu were clearly the next highest, with all elements down to Fe showing MF's greater than two. All the rest were smaller than one. MF is concentration in insect body divided by concentration in foliage. Studying the budworm's utilization efficiencies of mineral elements in a low-salt McMorran (1965) meridic diet gave nearly the same results as the above magnification factor array:

Cu>N>Zn>P>K>Mg>Fe>Ca>Mn

The utilization efficiencies array is somewhat different from MF array because the artificial diet does not exactly match the levels of elements contained in the foliage. The point is, though, that any variations in budworm performance on different hosts will most likely be due to variations in the limiting nutrients--those having highest magnification factors or utilization ratios.

Table 3.--Concentrations (ppm dwt) of mineral elements in the bodies of male and female spruce budworm adults, and balsam fir foliage (6/22/82), and the ratios of insect/foliage elemental concentrations

Item	%N	P	K	Mg	Ca	Zn	Fe	Na	Cu	Mn
SBW Female										
Mean	7.97	7,539	9,932	861	290	113	73	56	12	4
SD	.44	308	800	101	97	22	43	21	4	3
SBW Male										
Mean	9.51	9,569	10,855	987	340	117	87	128	19	6
SD	.40	642	892	83	73	23	51	38	8	4
Fir foliage										
Mean	1.26	1,872	12,738	927	3,671	34	31	9	4	303
SD	.10	108	1,704	109	646	4	4	2	1	103
♀SBW/foliage	6.3	4.0	.78	.92	.08	3.3	2.4	6.1	3.3	.01
♂SBW/foliage	7.5	5.1	.85	1.06	.09	3.4	2.8	13.9	5.4	.02

Growth in Relation to N and Mineral Elements

Balsam fir. Regressing male and female dry weights against the foliar elemental concentrations they experienced as fifth and sixth stage larvae revealed that nitrogen was the only variable consistently and positively related to growth (Table 4). Calcium had a significant positive effect on female weights in 1981 but this is probably spurious owing to the fact that the larvae need only about 300 ppm calcium or less in their diets and foliage has about 15-fold this level. Calcium, of course, could be related to some other important foliar variable which in turn affects larval growth. For example, it was negatively correlated ($p \leq .05$) with both tannins and phenolics. Calcium may form chelates with many kinds of phenolics, perhaps rendering them less deleterious to a leaf consumer. The effects of the other elements (K, Fe, Cu) were, to our surprise, all negative. For example, based on the body/foliage magnification factors, we expected that Fe and Cu were in relative short supply, but their negative correlation with weight gain implies otherwise. However, as in the case of calcium, their correlation need not imply direct cause and effect but some indirect effect. K, for example, was significantly positively correlated with 10 mono- and sesqui-terpene species in balsam fir and with the terpene grand sums. Fe, on the other hand, was negatively correlated with four terpenes and Cu positively with three. In general, all foliar elements tended to show a negative correlation with total phenols and condensed tannins.

Late season results were unlike the early season results in that K and Cu were now positively correlated with weight gain (Table 4). For both elements, however, late season levels were less on the average than they were in early season (e.g., K: 8000 vs. 10,482). Not only were they less, they were much more variable (e.g., CV-K = .22 vs. CV-K = .08). Late season Cu levels were probably below optimal, for more than half of the late season trees had less than 0.5 ppm in their foliage. Early season trees, on the other hand, averaged about 4 ppm--none going below 2.6 ppm. When Cu occurred at similar levels (4 ppm) in the meridic diet, budworms more completely (ca. 60-75 percent) extracted it than other elements that occurred at levels comparable to early season foliage. N was not a significant late season nutrient variable for both sexes but only for males, probably owing to its relatively uniform concentration among late season trees (CV-N = .08 vs. CV-N = .14).

Table 4.--Significant variables in the regression of mean male and female adult dry weights per tree on foliar mineral element concentrations in different host trees and years

Host species	Significant Variables				R^2	n[a/]
Females						
BFir-79	+N	-Fe			.69	12
BFir-81	+N	-Fe	-K	+Ca	.44	50
BFir-late	+K				.17	18
Males						
BFir-79	+N	-Cu			.47	12
BFir-81	+N	-Fe	-K		.18	50
BFir-late	+N	-Fe	+Cu		.33	18
Females						
WSpr-81	+N	-K	-Zn		.61	18
BSpr-81	+N	-K			.66	17
Males						
WSpr-81					00	18
BSpr-81	+N	-Mn	-Cu		.76	17

[a/] Number of trees in the regression.

Spruces. As with the firs, N was the only element showing a consistent, positive relation to weight gain for both sexes (Table 4). All other elements were negative; thereby corroborating the pattern seen for early season balsam fir. The consistently negative contribution of K stands out because K levels in black spruce were even lower in most cases than they were for late season balsam (6000 ppm vs. 8000 ppm). Thus one is obliged to conclude that K itself is not directly affecting weight gains but indirectly through its effect on some other plant traits. For example, plant K was positively associated with every terpene species but one in both black and white spruce. We hasten to add that none of the associations was statistically significant though. This is probably at least partially due to a small data set which will be enlarged in the next few months. As before, the negative contribution of Cu is difficult to explain because copper was close to its minimally optimal level in the foliage diet. On the other hand, manganese may be approaching deleterious levels in the foliage because it's about one-hundred fold more abundant there than in the insect's body. Moreover, excessively high levels of one mineral element can interfere with the absorption and utilization of other elements and nutrients (Maynard *et al.* 1979). No explanation is readily available for zinc's negative contribution because its level in the foliage (46 ppm) is hardly excessive. In fact, at this level in the artificial diet it is highly utilized and supports good growth.

Survival in Relation to N and Mineral Elements

Regressing generation survival (the arcsin transformation of the survival rate) against foliar elements revealed that none accounted for more than 50 percent of the observed variation and in most cases, they accounted for only about one-third of the variation (Table 5). Moreover, there was no consistency between years or between species. Therefore, we feel that the observed results may be entirely an artifact.

We were also surprised to learn that insect weight gains (FWT, MWT) and survival rates per tree were not significantly correlated with one another except on black spruce (*) where the relationship was negative ($p \le .05$) contrary to expectation:

	BFir	WSpr	BSpr	Late BFir
FWT	.11	.13	-.51*	.23
MWT	-.03	-.28	-.56*	.16

The latter result may suggest that foliage was in short supply and hence higher survival meant less food per insect and thus lower growth. On the other hand, it also could suggest that the tree traits governing survival and growth of budworm are linked in opposing directions, or perhaps not at all in the case of fir and white spruce.

Table 5.--Significant variables in the regression of generation survival rates per tree (2d→adult) on foliar mineral elements and phenolics (PH) in different host trees and years

Host species	Significant variables	R^2	n[a/]
BFir-79	+Fe -PH	.32	39
BFir-81	+Mn +Cu	.31	50
BFir-late	+N	.18	18
WSpr-81	+Cu -K -Fe +PH	.52	18
BSpr-81	+Mg	.33	18

[a/] Number of trees in regression

Budworm Performance in Relation to Allelochemics

Terpenes

Preliminary analyses reveal that several terpenes are significantly negatively correlated with weight gain for both sexes in both balsam fir and white spruce. In the case of balsam fir, the following six species of monoterpenes were negatively correlated ($p \le .05$) with growth except where noted (ns):

	alpha-pinene	beta-pinene	camphene	beta-phellandrene
MWT	-.36	-.37	-.43	-.38
FWT	-.32	-.32	-.40	-.25

	bornyl acetate	terpinolene	terpene grd sum
MWT	-.24	-.30	-.62
FWT	-.16 ns	-.24	-.45

None of the terpenes in balsam fir, in fact, were significantly positively correlated with growth.

In the case of the white spruce, five different compounds were significantly negatively correlated ($p \le .05$) with growth except where noted (ns) as shown in the following tabulation:

	camphor	Sesquiterpenes & monoterpene alcohols #1	#2	#14	#35
MWT	-.33 ns	-.69	-.19 ns	-.32 ns	-.57 ns
FWT	-.71	-.64	-.66	-.68	-.65

Only one terpene showed a positive relation to growth. The fact that white spruce and balsam may have different terpenes regulating budworm performance is not extraordinary because the two trees have different kinds as well as amounts of the individual terpenes. For example, balsam at mid-June had a terpene grand sum of about 6,700 ppm fwt vs. 836 ppm for white spruce. In other words, balsam has roughly 8-fold more terpenes. Black spruce was similarly terpene-rich having about 6,200 ppm fwt in mid-June. This suggests that if it's the total amount of terpenes that are deterent, then budworm performance should be better on white spruce than on either balsam fir or black spruce, all other things being equal. The data, however, show the contrary. What is the explanation? Particular species-unique terpene compounds may be especially deterent at low levels in white spruce (e.g., camphor). On the other hand, all other things are not equal. For example, lower plant nitrogen levels may make white spruce significantly less suitable than fir in spite of its lower terpene levels. White spruce, for example, had 20 percent less N in mid-June than did balsam fir (e.g., 1981: 1.24 percent vs. 1.52 percent). We know that this is due to the fact that white spruce grows faster than balsam fir and thereby dilutes its foliar nutrient levels similarly faster (Fig. 1).

Going back to the hypothesis of the effects of terpene grand sums on budworm growth leads us to differences between small and medium/large balsams. As we said earlier, small trees produced 10 to 20 percent smaller insects than did medium/large trees. This may have been due to the fact that small trees had 42 percent more terpenes than did medium/large trees at mid-June when larvae were in the 5th/6th instars (9,547 ppm fwt vs. 6,700 ppm). The N levels in these two age classes were nearly identical (e.g., 1981: 1.50 vs. 1.55), so this is not a large potential source of variation. We also know that mineral element differences are not a likely explanation of the difference because they appeared to be available in sufficient amounts in both age classes, barring any negative interactions with tannins and phenolics. Similarly, there were

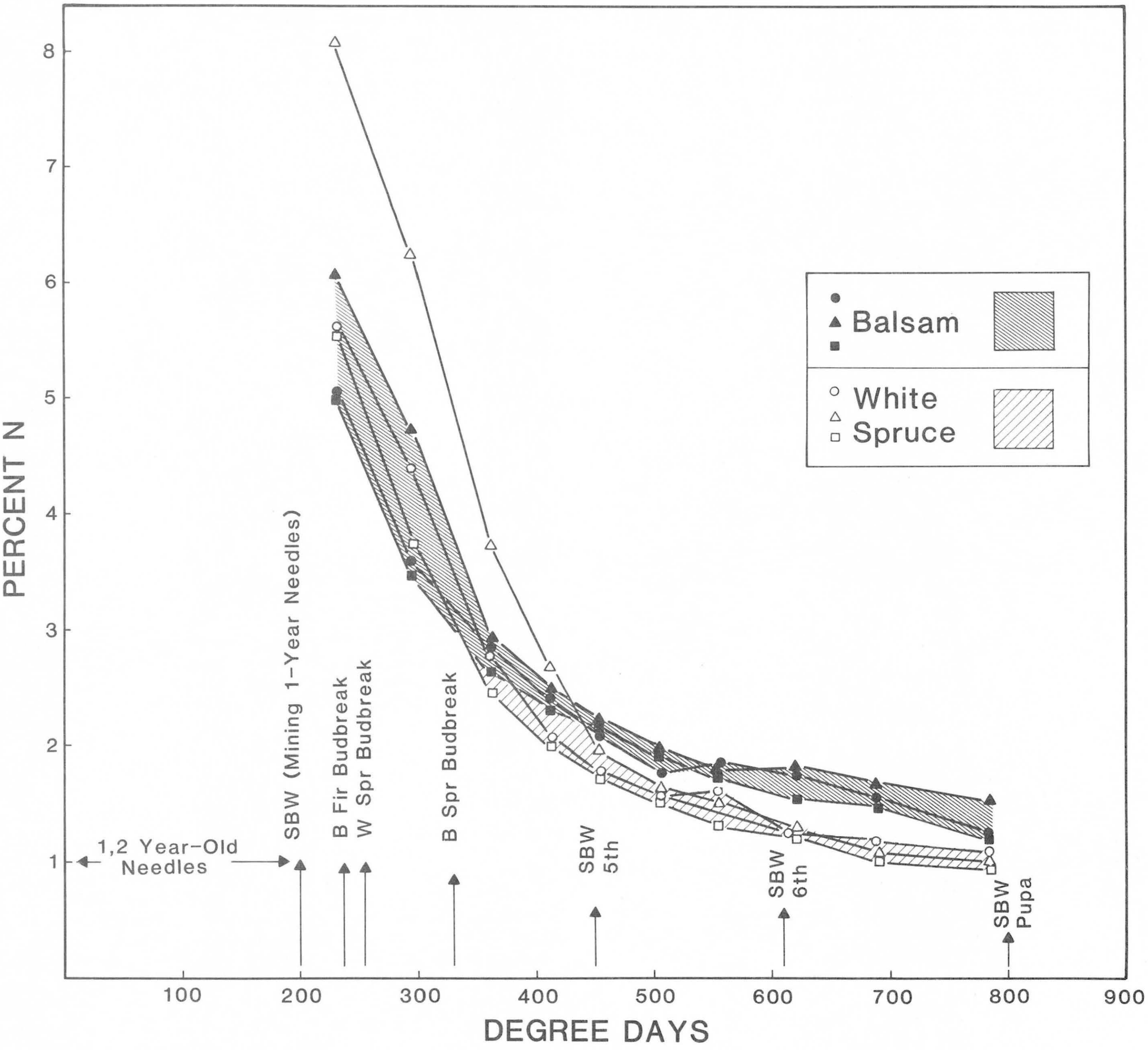

Figure 1.--Seasonal change in foliar nitrogen content (percent dwt) of three balsam and three white spruce with respect to degree day accumulations (2.8°C as base), and the phenology of the spruce budworm

no significant differences between the two groups for total phenols (2.64 percent vs. 2.59) or tannins (3.8 vs. 4.5 percent). Therefore, until the final analyses are complete, we suggest that the budworm growth difference between balsam age classes is due in large part to their terpene differences.

Small white spruce also had smaller insects and more total terpenes than did large white spruce (994 ppm fwt vs. 667 ppm). But, in this case, male and female weights were not correlated with terpene grand sums. The most likely explanation for differences in insect weight gain between white spruce age classes is the difference in levels of the one or more of individual terpene compounds listed above. There were no significant differences in tannins, total phenolics, and N levels between the two age classes just as was the case for balsam.

Phenolics-tannins

Incorporating phenolic and tannin estimates along with the mineral element data in the multiple regressions did not change any earlier conclusions for balsam fir but did in the case of male weight gain on white spruce. In this case, tannin was the only variable significantly correlated with male weight ($r = -.46$). This reflects the fact that no other variables were previously related to male weight gains.

The simple correlation coefficients between phenolics, tannins and weight gains on fir and spruce were not significant in all but two cases (*) as shown below:

	Balsam		White Spruce	
	FWT	MWT	FWT	MWT
Phenolics	-.29*	.00	.19	.02
Tannins	-.06	.13	-.20	-.46*

In general, levels of tannins and phenolics were negatively correlated with nearly all mineral elements in fir and white spruce. In the case of spruce, however, only one of the correlations was significant. This is in striking contrast to balsam where only five out of eighteen negative correlations were not significant in both 1979 and 1981, 2 years for which we have substantial data sets. The following tabulation shows the significant ($p \leq .05$) tannin and phenolic correlations with N in balsam fir foliage:

	N-79	N-81
Phenolics	-.62	-.45
Tannins	na	-.42

Palmer (1982) found the same negative relationship between phenolics and N in Populus tremuloides foliage.

Previous studies on the effects of phenolics and tannins on the growth performance (via lowered protein utilization) of folivorous insects have almost unanimously come to the same general conclusion: there seems to be little or no measurable deleterious effect, except perhaps at extraordinarily high tannin concentrations (Lawson et al. 1982, Bernays 1981, Fox and McCauley 1977). While our analyses are too preliminary to come to any firm conclusions, we believe that there may also be long-term, subtle effects that have been overlooked in the typical growth bioassays which usually measure insect performance (nutritionally and behaviorally) for only one or two instars, or at most for the whole feeding period of one generation. Tannins and/or phenols could have some chronic, subtle effects, such as through the chelation of micro-nutrients like Cu, Zn, and Fe--which then renders them less available to the insects. Such effects would have to be monitored over two or more successive generations to see the impacts of chronic micronutrient deficiencies. The chelation of such micronutrients may also be an important plant defense against microorganisms and could also thereby affect essential gut microbes or pathogens in those consumers having such microsymbionts (Swinburne 1981, Radhakrishnan and Sivaprasod 1980, Roy and Mukherjee 1979, Shieh et al. 1968, Emery 1982).

Budworm Growth Response to N Levels

The analyses have indicated that budworm weight gains are consistently but not exclusively linked to variations in plant foliar N levels. In those cases where N was not implicated, there was usually only very little variation in N levels among plants. Therefore, to add strength to the N hypothesis, we planned two experiments to raise the level of nitrogen offered to larvae, thereby hoping to elicit increased growth. The first experiment was designed to raise dietary N for just the first three instars (2, 3, and 4), whereas the second was designed to raise N for the whole larval life span, but particularly for late stage (5, 6) larvae.

Diet/Foliage Transfer Experiment

In the early spring before budbreak occurs, second stage budworm larvae mine 1-year-old or sometimes 2-year-old needles for 1 to 2 weeks (Blais 1979, McGugan 1954). After molting to the third instar, larvae then move to the newly opening buds or male flowers for feeding. During the needle mining period budworm subsist on very little N, such needles, usually having between 0.95 and 1.1 percent N. The newly flushed foliage, on the other hand, is very N rich (as high as 8 percent) but very emphemeral because shoots and needles are rapidly expanding thereby causing a precipitous decline in most foliar elements (Fig. 1), probably owing to a dilution effect. The decline takes the form of a negative exponential ($\%N = aX^{-b}$) as has also been reported by Shaw and Little (1977). By the fifth larval stage N levels are ≤ 1.5 percent in balsam, and somewhat less in white spruce owing to its faster development and nutrient dilution (Fig. 1). Since the fifth and sixth larval stages eat about 95 percent of the whole food budget for the larval period, (Retnakaran 1983, Miller 1977) we asked whether a consistently high N diet for the first three feeding stages (2, 3, 4) would have any enhancing effect on ultimate weight gain if these larvae were then transferred at the 5th instar to a low N foliage diet. To test this hypothesis we simultaneously grew insects on meridic diet (McMorran 1965) having about 4.4 percent N and also on the natural hosts, balsam and white spruce. At the fifth larval stage, ten females were transferred from the diet to each of 48 balsam fir and 20 white spruce trees for completion of feeding. At pupation all insects were removed and later weighed for adult body size. The results on balsam showed that diet/foliage reared larvae were significantly larger (9 percent) than foliage/foliage reared insects (20.51 vs. 18.87 mg). Furthermore, plotting mean female weights of each group from a tree against the foliar N values they experienced as fifth and sixth stage larvae gave nearly identical regressions except for the intercepts which reflect their mean differences in body size:

diet/foliage $\quad FWT = 12.06 + 5.42\%N \quad r^2 = .19$
foliage/foliage $\quad FWT = 10.37 + 5.46\%N \quad r^2 = .22$

Thus the early diet ration seems to have "bumped up" final adult weights.

On the other hand, the same experiment on white spruce gave opposite results; diet/foliage insects were about 9 percent smaller (14.18 vs. 15.50 mg where $.1 < p < .05$). There was no significant regression of either group on foliar N values but the two groups nevertheless performed similarly on the set of 20 spruce as evidenced by the significant regression between their respective mean adult weights:

$$FWT\ (d/f) = 6.72 + .481 \quad FWT\ (f/f) \qquad r^2 = .30$$

These results are in direct contrast with those reported by Thomas (this proceedings) who found that diet to current white spruce foliage transfers (at the 6th larval stage) produced larger insects (ca. 21 mg) than similar transfers to balsam fir (ca. 15 mg). The explanation for this divergence from our results could be due to several factors: different populations of insects, different physical environments, and different host materials. The latter one entails at least two variables. Thomas used excised branches of both fir and spruce whereas we used intact branches. Perhaps even more important is the fact that the eastern populations of white spruce and fir are known to differ (phytochemically) from the more western populations such as the one we studied in northern Minnesota (Wilkinson et al. 1971, von Rudloff 1975, Zavarin and Snajbeck 1972, and Lester 1974). For example, von Rudloff (1975) reported that camphor levels are nearly twice as high in some western populations of white spruce than in eastern ones. However, until more is also known about the nutrient levels of the eastern host materials, it's impossible to explain the causes of the apparent differences in budworm performance.

To recapitulate, the balsam fir transfer experiment suggested that giving young larvae a high protein diet enhanced their performance by an amount that was constant, when the N effect on late larvae was accounted for. On the other hand, the spruce transfer experiment suggested that the early high protein diet was not enhancing, for these larvae attained smaller size than those having spent their early instars on spruce. Nevertheless both diet and tree insect groups performed similarly with respect to the trees they were on. The following tabulation summarizes the transfer effects on adult female dry weights relative to the meridic diet control:

	diet/wsp	wsp/wsp	bfir/bfir
Mean female weight (mg)	14.18	15.50	18.87

	diet/bfir	diet/diet
Mean female weight (mg)	20.51	26-31

Obviously, feeding for the fifth and sixth larval stage on a tree was not as good as feeding on the diet. White spruce insects achieved about half, and balsam insects about two-thirds of their potential size. Why the meridic diet experience enhanced growth on fir but disenhanced it on spruce is an enigma. Perhaps early season spruce foliage is superior to the artificial diet. On the other hand, later in the season, it is plainly inferior. One can speculate that there must have been significant transfer shock going from diet to trees, especially in the case of white spruce. Perhaps the shock was due to higher metabolic costs to operate the budworm's mixed-function oxidase system on spruce than on fir (Brattsden 1983). This assumes, of course, that there were allelochemics that elicited higher MFO activity on spruce than on fir or that there were present significant MFO inhibitors in the spruce foliage which may have rendered spruce allelochemics more deleterious. On the other hand, the effect may have occurred at the behavioral level, for spruce foliage seems to harden off faster than balsam, and it might also possess important feeding deterrents (e.g., pungenin) (Heron 1965).

Fertilization Study

To elucidate the budworm growth response (ΔWT) to changes in foliar N (ΔN), we first regressed budworm weight gains in 1981 on foliar N levels. Secondly, we fertilized our most N-impoverished trees, the lowland black spruce (3-5 m tall and 30-45 years old) and half of the small balsam which are comparable to trees used in two earlier fertilization studies (Shaw et al. 1978, Shaw and Little 1972). In each case we had 15 treated and 15 control trees. We applied 600 lbs. N/acre (urea) around the root zone of each tree during the first week of May 1982.

Male and female weight gains (MWT, FWT) in 1981 were clearly linear functions of foliar N (using all tree species and age classes):

$FWT = 3.45 + 9.844\ (\%N) \quad r^2 = .54 \quad n = 114$
$MWT = 3.13 + 3.959\ (\%N) \quad r^2 = .44 \quad n = 113.$

Scatter plots of the data revealed that female weight gains showed a clear positive trend over the full range of N values (0.47-2.05%). Furthermore, female weights increased with even higher N levels (2-4%) administered in the form of casein and wheatgerm in artificial diets. Male weights, on the other hand, showed little tendency to increase with foliar N levels above 1.5%. Moreover, administering even higher levels of N (2-4%) in the artificial diet brought about a weak response, 1-2 mg, suggesting that above 1.5% N males have a shallow response potential if any.

The linear regressions imply that the weight gain response of budworms to an increment of N is constant, e.g., $\Delta FWT/\Delta N = 9.84$, the slope of the regression line. In other words, for each unit increase in foliar N there is a concomitant 9.8 mg increase in female weight. In the case of the fertilization study, our treatment of 600 lbs. N/acre elevated foliar N levels by 0.40 and 0.45% for the black spruce and balsam fir trees, respectively. These N changes both elicited 1.38 mg changes in female mean weights as shown in the in the following tabulation:

	FWT	ΔFWT	MWT	ΔMWT	%N	Δ%N
BfirCk	18.78	1.38	10.87	0.37	1.31	0.45
BfirF	20.16		11.24		1.76	
BSprCk	11.10	1.38	6.73	0.96	0.85	0.40
BSprF	12.48		7.69		1.25	

The urea treatment caused significant ($p \leq .05$) increases in female weights on both tree species but significant increases in male weights only on black spruce. The fact that the males did not respond to urea fertilization on balsam lends support to our suspicion that males have a low optimal dietary N requirement (perhaps about 1.5%) and that near this level their response is nearly flat.

Using the fertilization data for females only, we calculate that $\Delta FWT/\Delta N$ for balsam and black spruce are 3.07 and 3.45, respectively. These values are not much different from those derived from the fertilization experiments of Shaw et al. (1978). They reported that high and low urea treatments raised foliar N values (on June 23) by 0.8 and 0.4%, respectively. These increments in turn elicited female adult dry weight gains (using formula of Mattson et al. 1982) of 3.33 and 1.13 mg. Thus $\Delta FWT/\Delta N$ was 4.16 and 2.83 for the high and low urea treatments, respectively. Shaw et al.'s high calcium nitrate treatment gave a $\Delta FWT/\Delta N$ value of 2.86. Therefore, pooling Shaw et al.'s and our values suggests that $\Delta FWT/\Delta N$ averages about 3.27 and ranges from 2.83-4.16. In other words, $FWT = a + 3.27\ (\%N)$. This implies that for every 1% increment in foliar N, there will be a corresponding 3.27 mg dwt increment in adult female weights.

On the other hand, our earlier regression analysis suggested that $\Delta FWT/\Delta N$ should be about 9 instead of 3. What's the explanation for this discrepancy? The explanation might lie in the fact that changing foliar N through fertilization results in many other changes in foliar chemistry that are not all enhancing. For example, fertilization is also known to raise the levels of mono- and sesqui-terpenes. Moreover, the fertilization studies reported herein (Shaw et al. and ours) were done on young balsam fir which we have already shown to have significantly higher terpene levels than older trees. Thus the budworm responses (ΔFWT) on small trees might be significantly less than on older trees which have lower levels of terpenes. Similarly, the lowland black spruce which we fertilized probably has levels of terpenes at least as high and total phenolics levels that are higher than the small fir. Thus the overall 1981 regression may have a higher slope or predicted weight increment per unit of N because the pooled data consists of such species as white spruce and medium/large balsam which may have higher levels of N relative to terpenes, thereby giving higher weight gains per unit N increment than would small balsams and lowland black spruce.

Changes in Fecundity

In order to obtain some idea of the potential impact of different dietary regimes on budworm population dynamics, we used the fecundity/pupal size equation of Miller (1963) and the adult dry weight/pupal size equation of Mattson et al. (1982) to project changes in female dry weight into changes in egg output. The resulting formula for fecundity in relation to body size is as follows:

$$F = -442.1 + 216.7\ (FWT)^{.37}$$

$$\Delta F = 81.04\ (FWT^{-.63})\Delta FWT$$

The second equation says that changes in egg output (ΔF) increase directly with changes in body size (ΔFWT). In other words, a 2 mg change in body size elicits exactly twice the output of a 1 mg change and so on, holding initial body size (FWT) constant.

The question yet to be answered is how large are the differences in fecundity between insects having different sizes. For example, female budworms from small balsam averaged 32 less eggs than similar females on medium balsam (187 vs. 219) (Table 6). Similarly insects from small white spruce averaged 26 less eggs than females from large white spruce (148 vs. 174). In the case of black spruce, females from the lowland trees averaged 117 fewer eggs than those from upland trees (32 vs. 149).

In the case of the fertilization experiments, we estimated that increasing foliar nitrogen levels by 1.0% would result in roughly a 3 mg increment in female weight. This translates into 41 more eggs for females that weighed 17 mg before fertilization. If foliar N increased only 0.5%, the result would be about half as many eggs, i.e., 20 more per female.

The significance such differences in egg output have on the insect's population dynamics cannot, of course, be answered. These are questions that must be addressed through an ecosystem level model which incorporates all of the major factors regulating budworm natality and mortality.

CONCLUSIONS

Although the study is not yet completed, there are some consistencies that seem substantial enough to warrant recapitulation.

There are clear differences in budworm growth between small and large tree classes, larger trees producing larger and hence more fecund insects. Furthermore, there are differences between species--balsam giving rise to larger insects than white spruce. This pattern seems not to hold in eastern North America where the reverse is true. The explanation for this inconsistency may reside in the fact that the phytochemistry of the eastern and western tree populations are different owing to limited gene exchange, different geological histories, and different environments. There is also, of course, the possibility that the insect populations are substantially different as well.

Budworm survival rates did not vary among tree size/age classes and appeared to be highest on balsam and lowest on black spruce. Survival rates and budworm weight gain per tree were not correlated except in the case of black spruce where the association was negative. This implies that the plant traits which affect weight gain are independent of those that affect survival except perhaps in black spruce where they could be negatively linked. Budworm survival rates were not consistently linked to any variables that were measured.

Insect weight gains per tree were consistently, positively linked to foliar N and negatively to Fe and/or K. The negative associations with Fe and K are surprising because neither element occurs at levels high enough to be minimally optimal much less toxic or noxious. Nevertheless, iron levels in the insect body show a tendency to decrease with increasing levels in the diet. Iron, in fact, is the only element showing this inverse behavior. Moreover, iron concentrations in the insect are also negatively correlated with insect size. What this implies is not clear. It may mean that insects sequester less Fe per unit body weight when diets are better for growth. Fe concentration is also positively correlated with (1/N) of the diet. Since total consumption is usually positively linked to (1/N), Fe uptake by the insect may be related to the total amount of Fe passing through the digestive system.

Potassium levels by themselves may not be inhibitory to budworm growth but K is linked positively to foliar terpene levels which apparently are inhibitory.

Terpene levels were negatively linked to budworm weight gains both on balsam and on white spruce. In the case of balsam, terpene grand sums (all molecular species pooled) showed the strongest correlations whereas in white spruce individual compounds not the grand sums had the highest linkage to weight gain. Difference in budworm performance between tree age classes may be largely due to higher levels of terpenes in the younger trees. Because plant terpene profiles are known to exhibit significant east-west variation across North America, it is likely that budworm performance on these trees will similarly vary.

The significance of phenolics and tannins in the performance of spruce budworm is still uncertain. The early data suggest little effect on either survival or weight gain. However, the spectrum of phenolic compounds in balsam and the two spruces has not yet been examined so it is entirely possible that one or more of them could have significant behavioral or physiological effects. Pungenin, for example, in white spruce could be an important feeding deterent.

Finally, it is clear that changing insect N intake through artificial diet to foliage transfers and fertilization results in enhanced insect growth, at least on balsam fir. The data suggest that growth increment per unit nitrogen increment (ΔFWT/ΔN) is about 3, as long as the minimally optimal level of N in the diet has not yet been reached. We suspect that the growth increment per unit nitrogen increment (ΔFWT/ΔN) will vary with different host species and age classes owing to different background levels of nutrients and allelochemics.

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LEAF QUALITY AND THE HOST PREFERENCES OF GYPSY MOTH IN THE NORTHERN DECIDUOUS FOREST

Martin J. Lechowicz

Associate Professor of Biology,
McGill University,
1205 Avenue Dr. Penfield,
Montréal, Québec
CANADA H3A 1B1

ABSTRACT

Both gypsy moth host preferences and the foliage characteristics that have been implicated as factors in host selection were monitored from 1979 to 1982 in a Quercus-Acer-Ostrya forest near Montréal, Québec. The preliminary analyses of these data suggest the hypothesis that gypsy moth larvae preferentially attack trees that have high sugar:tannin ratios in their young foliage.

The gypsy moth, Lymantria dispar L., is recognized as unusually polyphagous both in its native Eurasian habitats and also in eastern North America where it is introduced. Of the approximately 185 trees native to Europe (Polunin and Everard 1976) gypsy moth larvae have been reported to feed on the foliage of 75 (Kurir 1952; Györfi 1960). Similarly in the forests of northeastern North America where the gypsy moth has become established, the larvae can feed on at least 86 (Mosher 1915; Forbush and Fernald 1896) of the approximately 169 available native trees (Little 1979). Such a high degree of polyphagy among tree-feeding macrolepidopterans is matched by only a very few species (Fig. 1). This potential breadth of diet combined with the fact that not all trees are equally preferred as hosts (Lechowicz and Jobin 1983) makes the gypsy moth especially useful in developing and testing hypotheses about the interactions between woody plants and the herbivores that feed on their leaves. The gypsy moth essentially provides a bioassay to call attention to traits that make trees better or worse hosts to defoliating insects. If we can understand the basis for gypsy moth host selection, we may hope to gain some general insights into the forest defoliator-host interaction, particularly into the causes and potential control of insect outbreaks leading to catastrophic defoliation.

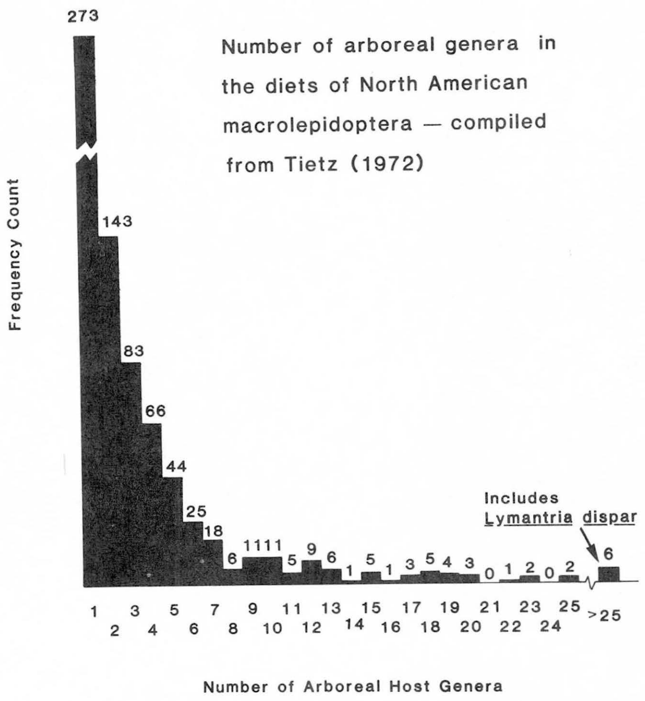

Figure 1. Numbers of genera of trees acceptable in the diets of North American macrolepidopterans; compiled from Tietz (1972).

Two general types of explanation have been put forward as mechanisms underlying host selection by lepidopteran larvae. These may be distinguished as behavioral versus ecological explanations. Behavioral explanations focus attention on proximate cues involving repellent and attractant compounds that influence larval feeding behavior; this approach most often draws on evidence from laboratory feeding trials and neurophysiological monitoring of sensilla exposed to test compounds. Dethier (1982) provides an interesting historical review of this literature. Ecological explanations focus attention on the nutritional quality of potential host foliage and assume that natural selection has led to preferences for hosts with relatively nutrient-rich foliage low in toxic or digestibility-reducing compounds. Although such ecological explanations have a long history (see Futuyma 1983 for a recent review) they received increased attention after Feeny (1976) and Rhoades and Cates (1976) independently proposed a general theory of plant defense against herbivores. These two types of explanation are not mutually exclusive; evolution should generally lead to proximate behavioral cues which result in larvae feeding on hosts of high nutritional quality.

In the work described in this paper I have taken an ecological rather than behavioral approach to attempt to understand the basis of larval host preferences in the gypsy moth. Working in a forest southeast of Montréal, Québec, which is near the northern limit of both the deciduous forest and the gypsy moth in North America, I initiated a long term study of gypsy moth host selection and of various tree characteristics which have been suggested to influence host selection by lepidopteran folivores. Here I describe the studied forest, summarize the history of its infestation by gypsy moth, explain the methods which have been used

TABLE 1. Phytosociological Summary of the Tree Stratum on the Southern Faces of Lake Hill, Mont. St. Hilaire, Québec.

Tree Species	Common Name	Acronym	Frequency[a]/	Density[b]/	Dominance[c]/	Relative Importance Value[d]/
Acer pensylvanicum L.	Striped maple	Apen	1	1	8.5	0.3
A. rubrum L.	Red maple	Arub	1	3	67.7	0.5
A. saccharum Marsh.	Sugar maple	Asac	24	158	2344.4	17.0
A. spicatum Lam.	Mountain maple	Aspic	1	4	39.2	0.5
Amelanchier sp.	Serviceberry	Amel	3	3	27.4	0.9
Betula papyrifera Marsh.	White birch	Bpap	9	47	696.3	5.5
B. lutea Michx. f.	Yellow birch	Blut	1	4	60.7	0.5
Carya cordiformis (Wang)K. Koch	Yellowbud hickory	Carya	2	2	35.6	0.6
Fagus grandifolia Ehrh.	Beech	Fagus	7	78	1373.2	7.6
Fraxinus americana L.	White ash	Frax	17	56	778.5	8.1
Juglans cinerea L.	Butternut	Jug	2	2	71.8	0.7
Ostrya virginiana (Mill.)K. Koch	Ironwood	Ostrya	20	181	1835.3	15.7
Pinus strobus L.	White pine	Pinus	3	4	92.4	1.1
Populus grandidentata Michx.	Big-tooth aspen	Pgran	2	11	206.1	1.4
Prunus pensylvanica L.f.	Pin cherry	Ppen	1	3	27.2	0.5
P. serotina Ehrh.	Black cherry	Pser	2	2	29.0	0.6
Quercus rubra L.	Red oak	Qrub	22	341	6963.8	33.3
Ulmus rubra Muhl.	Slippery elm	Urub	1	1	15.4	0.3
Tilia americana L.	Basswood	Tilia	12	22	357.5	4.7
Summations			131	923	15030.0	99.8

[a]/ Frequency: The number of $500\ m^2$ quadrats in which each tree species occurred; total sample was 24 quadrats.

[b]/ Density: The number of stems of each tree species found in all 24 quadrats.

[c]/ Dominance: The cumulative DBH in cm. for each tree species summed in all 24 quadrats.

[d]/ The mean of frequency, density, and dominance each relativized as a percentage of the respective total for all species; see Curtis (1959).

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to quantify host preference, and detail the tree characteristics which were monitored over the period 1979 through 1981. I then present a preliminary analysis of these data and suggest a tentative explanation for the dynamics of the interaction between the gypsy moth and its host plants.

The Lake Hill Study Site

The work described here concerns a gypsy moth infested forest on Mont St. Hilaire, one of the eight Monteregian Hills which rise abruptly from the plains of the St. Lawrence River Valley in the vicinity of Montréal, Québec (Fig. 2). Mont St. Hilaire consists of seven low peaks surrounding a small lake; the peaks rise to a maximum of 416 meters, about 355 meters above the surrounding plain which is a mosaic of villages, agricultural land, and remnant woodland. The mountain itself is covered by forest which in many areas has been little or not at all disturbed for over 300 years; topographic and edaphic heterogeneity contribute to a diversity

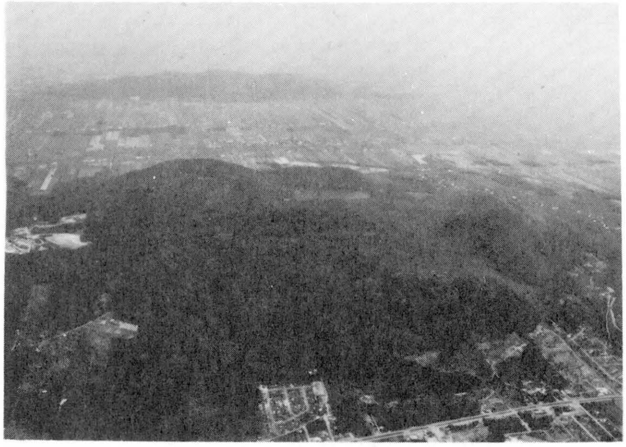

Figure 2. Aerial view of Mont St. Hilaire, looking southeast toward Rougemont. Lake Hill rises from the south shore of Lac Hertel in the center of the figure. Photo courtesy of Dr. Luc Jobin, Laurentian Forest Research Centre, Ste. Foy, Québec.

of habitats including old growth beech-maple forests on deep moist soils, hemlock on steep rocky slopes, yellow birch-red maple swamps in depressions, oak-dominated forests on the dryer sites, and successional forests with aspen and birch on recently disturbed sites (Phillips 1972). Comparable forests have existed in this area for the past 8000 years (Richard 1977). Maycock (1961) provides a thorough summary of the geology, soils, climate, and flora of Mont St. Hilaire and Walther (1963) describes the vegetation of all the Monteregian Hills.

The forest in which gypsy moth activity has been primarily monitored is on the southern and western faces of Lake Hill, one of the lower peaks of Mont St. Hilaire which reaches an altitude of only 297 meters. The composition of this forest was determined by randomly placing twenty-four 500 m^2 circular quadrats along 4 altitudinal isoclines at about 25 m intervals down from the ridge top. In each quadrat the diameter at breast height (DBH) and the species of all trees (DBH $\geq$ 0.8 dm) were recorded. These data are summarized in Table 1. The relative importance values (Curtis 1959) emphasize the dominance of Quercus rubra, Acer saccharum, and Ostrya virginiana in this forest; Fraxinus americana, Fagus grandifolia, Betula papyrifera, and Tilia americana are also substantial components of the tree stratum but the remaining eleven tree species are of only minor importance. Tsuga canadensis, Populus tremuloides, P. balsamifera, P. deltoides and Betula populifolia occur sparsely on Lake Hill but were not found in the random quadrats.

Compared to the forests of the St. Lawrence Valley and southern Québec in general (Grandtner 1966; Bouchard and Maycock 1978) the Lake Hill forest is xeric. Detailed studies of the annual heat and water budgets of the south versus north slopes of Lake Hill are available (Rouse and Wilson 1969; Wilson 1970). The oak-dominated forest on the south slope is decidedly more prone to summer drought stress than the beech-maple forest on the north slope. Such topographic juxtaposition of mesic and xeric forest communities is common on the Monteregian Hills (Walther 1963). Xeric forests are generally more susceptible to attack by gypsy moth (Houston and Valentine 1977).

History of Gypsy Moth at Mont St. Hilaire

The gypsy moth appears to have first become established in Québec during the mid-1960's (Cardinal 1967; Brown 1967) and until the mid-1970's serious infestations were limited primarily to Huntingdon and Chateauguay counties south and west of Montréal (Martineau et al. 1975). About 1975 the zone of serious infestation began a steady expansion (Fig. 3); in 1975 traces of gypsy moth were noted on Mont. St. Gregoire, one of the Monteregian Hills south of Mont St. Hilaire (Martineau et al. 1976).

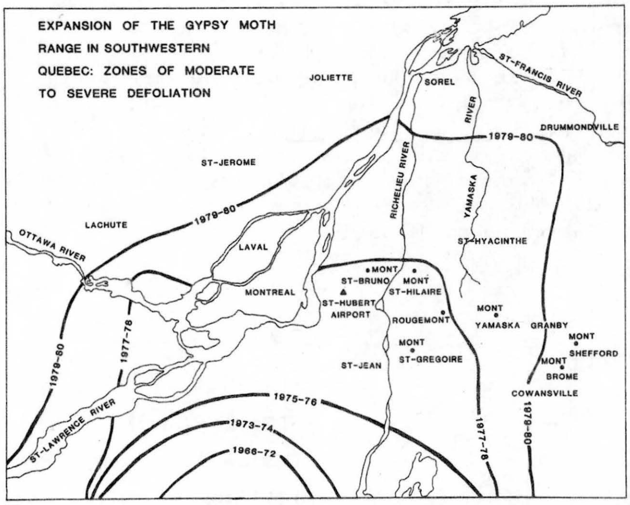
EXPANSION OF THE GYPSY MOTH RANGE IN SOUTHWESTERN QUEBEC: ZONES OF MODERATE TO SEVERE DEFOLIATION
JOLIETTE
SOREL
ST-FRANCIS RIVER
DRUMMONDVILLE
1979-80
RIVER
ST-JEROME
RICHELIEU RIVER
YAMASKA
LACHUTE
1979-80
OTTAWA RIVER
LAVAL
ST-HYACINTHE
MONTREAL
MONT ST-BRUNO
MONT ST-HILAIRE
ST-HUBERT AIRPORT
ROUGEMONT
MONT YAMASKA
GRANBY
MONT SHEFFORD
1979-80
1977-78
MONT ST-GREGOIRE
ST-JEAN
MONT BROME
COWANSVILLE
ST-LAWRENCE RIVER
1975-76
1973-74
1966-72
1977-78
1979-80

Figure 3. Approximate timing of expansion of the zone of serious gypsy moth infestation in Québec; adapted from information in Brown (1967), Cardinal (1967), Martineau et al. (1975, 1976), Lavallee et al. (1977, 1978), and Lachance et al. (1979, 1980, 1981).

There was no record of gypsy moth, and certainly had been no substantial defoliation, on Mont St. Hilaire until 1977 when 10 hectares of the forest on Burned Hill which is on the southwest face of the mountain were severely defoliated[1]. It is likely that the infestation had been newly established only in the preceding few years; this slope of the mountain faces a public campground which may have been the source of infection through vehicular transport from areas to the south or west. By 1978 the infestation had spread to 259 hectares of which 195 were severely defoliated. This area included 123 hectares of the Lake Hill study site most of which was heavily defoliated in 1978. It is noteworthy that serious infestations were limited to the more xeric forests on Mont St. Hilaire in accord with Houston and Valentine's (1977) comments on the characteristics of sites most susceptible to gypsy moth infestations. As part of his doctoral research Madrid (1979; Madrid and Stewart 1981) monitored gypsy moth populations on Lake Hill in 1977 and 1978; his data provide a very useful supplement to my records which do not begin until 1979. In addition government agencies[2]/ monitored the population on Lake Hill in 1978 and also in 1979 (Jobin 1982). Figure 4 summarizes the available information on gypsy moth population density at Lake Hill from 1977 through 1982. It is important to note that the population decline beginning in 1979 was not due to Québec's program of spraying *Bacillus thuringiensis* (Jobin 1982); the Lake Hill study site is on land owned by McGill University and protected as a UNESCO Man and Biosphere Ecological reserve in which spraying has not been allowed.

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[1] Jobin, L. (1978). Historique et situation actuelle de la spongieuse au Mont St. Hilaire, Internal report, Laurentian Forest Research Centre, Ste-Foy, Québec 13p.

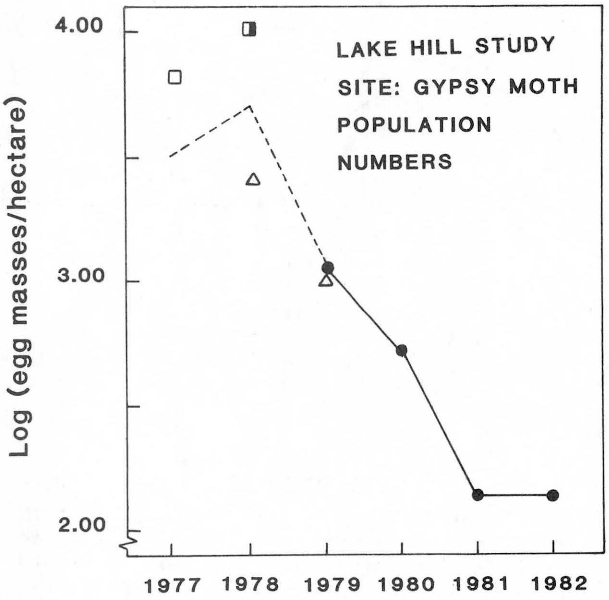

Figure 4. Gypsy moth population dynamics on Lake Hill. The squares are 1977 and 1978 data from Madrid (1979). The 1978 estimate by the government[2]/, shown as a half-closed square, is virtually identical to that by Madrid. The open triangles are data from Jobin (1982) in 1978 and 1979. All these plots were on the west end of Lake Hill, while my data (closed circles) also include the southern faces of Lake Hill.

Estimates of Gypsy Moth Host Preferences

The host preferences of late instar gypsy moth larvae on Lake Hill have been monitored from 1979 through 1982 using the method described in Lechowicz and Jobin (1983). This method measures preference as a function of the availability and the utilization of foliage on the different host trees in the forest. Emphasis is on the host preferences of late instar larvae which are primarily responsible for foliage losses (Valentine and Talerico 1980). If dispersing gypsy moth larvae actually had no preference for or against the foliage of a particular tree they would be expected to feed on that tree in direct proportion to its abundance in the forest canopy. This null expectation is founded on the assumptions that the probability dispersing larvae will encounter a host is determined by the host's relative abundance in the canopy and that larvae without preferences will settle on the first host they encounter. At dispersal larval preferences in the field should be closely related to the preferences reported in the behavioral literature which are determined in laboratory choice-trials (Mosher 1915; Barbosa *et al.* 1979). The late instar preferences reported here, however, arise not only from behavioral choices during dispersal but also from possible differences in early instar survival on different hosts. Larval survival may be controlled not only by foliage quality but also by bark roughness, canopy architecture, and similar traits that influence vulnerability to predators and parasites. These late instar host preferences are perhaps best viewed as measures of host susceptibility to defoliation by gypsy moth.

As discussed in detail by Lechowicz and Jobin (1983), the availability $\underline{p_i}$ for host i is measured by its contribution to the total DBH of the m different hosts in the sampled forest:

$$\underline{p_i} = \sum_{j=1}^{n_i} b_{ij} \Big/ \sum_{i=1}^{m} \sum_{j=1}^{n_i} b_{ij} \qquad \text{eq.1)}$$

where b_{ij} is the DBH of the jth tree of species i. Utilization is estimated from the mean of repeated counts of numbers of late instar larvae congregating under tarpaper bands around each tree in the sampled quadrats; this is a standard method to estimate numbers of late instar larvae feeding on a tree (Weseloh 1974). This estimate assumes that late instar migration between trees does not occur during the counting period; in low density populations this assumption appears to be met (Lechowicz and Jobin 1983; Mauffette and Lechowicz[3]/; Wallner, this volume). The utilization $\underline{r_i}$ of host i is measured by the number of larvae on host i relative to the total number of larvae on all the sampled hosts:

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[2]/ Bordeleau, C., C. Gagnon, C. Theriault, L. Jobin, C. Coulombe, and A. Caron (1980). Evaluation du programme de traitement au B.T. effectué contre la spongieuse au Québec en 1979, Internal Report, Ministre de Agriculture, Québec 37p.

[3]/ Mauffette, Y. and M.J. Lechowicz. The influence of host plant on the larval development rate of gypsy moth, *Lymantria dispar* (L.), in the forest environment, manuscript in review.

$$\underline{r}_i = \sum_{j=1}^{n_i} l_{ij} \Big/ \sum_{i=1}^{m} \sum_{j=1}^{n_i} l_{ij} \qquad \text{eq. 2)}$$

where l_{ij} is the mean number of larvae counted on the jth tree of species i.

Since gypsy moth larval growth and development differs on different host species (Schmidt 1956; Barbosa and Capinera 1977), the timing of larval counts to achieve a representative estimate of r_i is important. If a count is taken too early, larvae on some hosts will not have reached instar IV when the diurnal resting behavior on which the tarpaper counts depend begins (Leonard 1970). Conversely counts taken too late will miss larvae that have already pupated. Mauffette and Lechowicz[3]/ have analyzed the time course of larval numbers on 29 host species at 13 sites in southwestern Québec; in general there is about a 2 to 3 week window during which the mean of repeated counts will provide a representative estimate of late instar larval numbers across host species. It is desirable to make a fairly long series of counts and then discard the early and late entries which indicate that resting behavior is not developed on all hosts or that substantial pupation has occurred on some hosts. The preferences reported here are based on counts made on June 26-27 and July 3-4, 1979; on June 22 and 30, 1980; on June 21, June 29, and July 5, 1981; and on June 22, June 30, July 6 and July 14, 1982.

Several different algorithms are available to calculate preference from these measures of availability and utilization (Lechowicz 1982). Most give comparable results and differ primarily in convenience of interpretation. Here I have used Vanderploeg and Scavia's (1979a, 1979b) E* electivity index and their related selectivity index W. The selectivity for tree species i is:

$$W_i = (\underline{r}_i/\underline{p}_i) / \sum_{i=1}^{m} (\underline{r}_i/\underline{p}_i) \qquad \text{eq. 3)}$$

and the electivity for species i is:

$$E_i^* = (W_i - 1/n)/(W_i + 1/n) \qquad \text{eq. 4)}$$

where n is the number of potential host species. The selectivity W ranges from zero to one, a useful property in certain statistical analyses but not clearly indicative of preferred versus avoided hosts. In general, as a summary preference index, the E* electivity is easiest to interpret: E* is zero if the larvae feed randomly on a host, approaches minus one the more they avoid a host, and plus one the more they prefer a host. Lechowicz (1982) discusses the interrelationships and properties of all the available preference indices.

Monitoring of Host Foliage Characteristics

Many foliage characteristics have been implicated as possible factors determining the favorability of trees as hosts to lepidopteran folivores. Investigators have tended to focus on only one or a few factors in a given study despite the likelihood that a number of factors interact to control the susceptibility of a tree to herbivore attack. Certainly no single factor has proven to be even a reasonably universal predictor of herbivore susceptibility in woody plants. Also the predictable correlations between certain traits that may arise from constraints imposed by tree physiology and architecture can only be understood in a multifactorial analysis. Therefore within logistic limitations we have attempted to monitor a comprehensive set of foliage characteristics (Table 2) that may play a role in host selection by the gypsy moth. Sampling was concentrated on the spring foliage coincident with dispersal of gypsy moth and on the mid-summer foliage available to the late instar larvae. Samples were taken from a total of 23 tree species on Lake Hill but only 14 species both having adequate replication (3-6, mostly 5 or 6) and having been and having been included among the 19 species in the quadrats analyzed for host preference patterns are reported here. In the following paragraphs I briefly rationalize my choice of foliage characteristics and describe the methods used to assay them.

Leaf Toughness

Feeny (1970) demonstrated that the peak numbers of lepidopterans feeding on oak foliage coincided with the availability of tender, young leaves in the spring. For gypsy moth Hough and Pimental (1978) showed that larvae develop less well on the older, tougher leaves of host trees. Consequently toughness was monitored by Feeny's (1970) method which measures the mass required to shear the leaf tissue in an area between the main veins of the leaf. The shearing face of the penetrometer was 0.145 cm^2. In 1979 sand was used to add mass but subsequently water delivered through a pipette tip was found to give more reproducible results. Four replicate measurements of toughness were made on freshly harvested leaves.

Leaf Water Content

Scriber and Feeny (1979) have shown a correlation between higher leaf water content and better larval growth in lepidopteran larvae feeding on leaves of woody plants. Scriber and Slanksy (1980) review the importance of water content in effecting insect growth. The results of Hough and Pimental (1978) on gypsy moth larvae also indicate the favorability of high water content. The fresh and oven-dry weights of newly harvested leaves were used to calculate water content as a percentage of fresh weight at harvest; this is the normal practice in the entomological literature in contrast to the expression of water as a % dry weight common in the botanical literature.

Table 2. Foliage characteristics monitored from 1979 through 1981 at Lake Hill on Mont St. Hilaire, Québec. Rows designate date and Julian day of actual samples and the tabled entry indicates how samples were combined to represent spring or summer leaf condition in each year. Unsampled characteristics are indicated by n.d. In addition daily phenological records were kept in 1980 and 1981 during the period of canopy development.

	Toughness	% Water	% Nitrogen	Folin-Denis Phenolics	Precipitable Tannins	Leucoanthocyanins	Leaf pH	Leaf Buffer Capacity
1979								
May 14 (Day 134)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
May 21 (Day 141)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
June 4 (Day 151)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
July 18(Day 199)	summer	summer	summer	summer	n.d.	summer	n.d.	n.d.
1980								
May 27 (Day 148)	spring	spring	spring	spring	spring	spring	spring	spring
June 18(Day 170)	summer	n.d.	n.d.	summer	n.d.	summer	n.d.	n.d.
July 16(Day 198)	summer	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
1981								
June 1 (Day 152)	spring	spring	spring	spring	spring	spring	spring	spring

Leaf Nitrogen Concentration

McNeil and Southwood (1978) and Mattson (1980) review the considerable support for the critical importance of nitrogen availability to the growth of lepidopteran larvae feeding on the foliage of woody plants. The nitrogen concentration of oven-dry leaves was determined by a Kjeldahl analysis for total organic nitrogen (Bradstreet 1965) involving a sulfuric acid digestion in the presence of selenium catalyst and K_2SO_4 without any predigestion to reduce inorganic nitrogen. The resulting digest was then Nesslerized (Middleton 1960) and assayed colorimetrically for ammonia. Pace et al. (1982) have reported problems with nitrate reduction even in the normal Kjeldahl digestion but since tree leaves are extremely low in inorganic nitrogen (Van Tuil 1965) the nitrogen assayed here should be only that in forms available to lepidopteran larvae.

Leaf Concentrations of Various Phenolic Compounds

Many authors have taken the view that phenolic compounds function as important defenses against folivores, especially in woody plants (see particularly the reviews by Levin 1971; Feeny 1976; Swain 1978; Rhoades 1979; and Futuyma 1983). This view has not gone unchallenged, particularly by those who emphasize the many metabolic roles of phenolic compounds (Seigler and Price 1976) and those who question the efficacy of such putative defenses (Fox and McCauley 1977; Bernays 1978; Moran and Hamilton 1980; Martin and Martin 1983). This debate is aggravated by the extreme chemical diversity of phenolic compounds (Ribereau-Gayon 1972; Swain 1979) and the inadequacies of available assays for different groups of phenolic compounds. The latter problem has been recently reviewed but without a fully satisfactory conclusion (Horvath 1981; Martin and Martin 1982; Tempel 1982). Despite these problems, the unresolved controversy on the role of at least some types of phenolic compounds as defenses against herbivores requires their consideration here.

In the face of current methodological problems, I have settled on three assays for different phenolic fractions likely to have interpretable relationships with observed gypsy moth activity: 1) a Folin-Denis assay for total phenolics (Rosenblatt and Peluso 1941; Swain and Hillis 1959), 2) a leucoanthocyanin assay for condensed tannins (Swain and Hillis 1959 as modified by Govindarajan and Mathew 1965), and 3) a newly developed assay for phenolic compounds that bind to isinglass, a partially purified collagen from fish swim bladders often used to remove phenolic impurities from wine. The first two assays are well established. The isinglass assay is related to traditional tannin assays in the leather industry (Horowitz 1970), Marigo's (1972) absorption on gelatin, or Martin and Martin's (1982) recent modification of Bate-Smith's (1973) hemeanalysis. In all these methods Folin-Denis assays are made on an extract before and after exposure to a test protein to which tannins will bind, hopefully leaving only simple phenolics in solution. The difference in initial and final absorptance is then taken as a measure of biologically active tannins. Ideally the binding substrate should be leaf protein from each of the tree species being studied (Martin and Martin 1983) but this is virtually impossible in most studies. Recent discussions (Martin and Martin 1982; Tempel 1982) agree that at least some type of precipitable tannin assay should be included in ecological studies because such an assay directly measures the ability of tannins to bind protein, the supposed basis of their role in plant defense. In all three of the assays used here I have expressed results as simple absorptance values for lack of appropriate calibration standards (Martin and Martin 1982). This does raise the practically unavoidable possibility in this cross-species comparison that absorptance will not be an unbiased quantitative index of actual phenolic concentrations because of qualitative differences in the absorption spectra of constituent phenolics on the different tree species.

One further aspect of these phenolic assays which has received too little consideration in the literature is the method of extraction of phenolic compounds from harvested leaf tissues. It is clear that different extraction solvents will differ in both the quantities and quality of phenolic compounds recovered (Ribereau-Gayon 1972). In 1979 we extracted 0.1 gr oven-dry (70-80°) weight of powdered leaf tissue with an 80% methanol acid 1% HCl solution for 24 hours in a soxhlet apparatus. In subsequent years the method of Swain (1979) was adopted in which 0.1 gr oven-dry (40-50° to lessen degradation of compounds during drying) weight of powdered leaf tissue was extracted three times in hot (80°) 50% methanol. Test extractions of fresh frozen rather than dried leaf tissue did result in higher absorption per unit dry weight in both the Folin-Denis and leucoanthocyanin assay but the readings were significantly positively correlated (FD: $r = 0.26$, $p = 0.029$; LA: $r = 0.35$; $p = 0.003$). The problems and potential errors inherent in taking truly parallel samples to estimate the equivalent dry weight of frozen samples makes the direct assay of dry tissue preferable in this comparative study.

Leaf pH and Buffer Capacity

Berenbaum (1980) has shown that caterpillar species feeding on leaves of woody plants have higher gut pH than those feeding on herbaceous plants. She reported a mean midgut pH of 8.67 for larvae feeding on woody plants, significantly higher than the pH 8.29 mean for species feeding on herbaceous foliage. She suggested that the high gut pH of caterpillars feeding on woody plant foliage would serve to break up tannin-protein complexes thus rendering the tannin-based leaf defenses postulated to be widespread in woody but not herbaceous plants less effective. On a dry weight basis the hydrolyzable tannins are considerably more effective at complexing with proteins than the condensed tannins (Swain 1978), but the hydrolyzable tannin-protein complexes are less stable than those formed by condensed tannins (Goldstein and Swain 1965). Dissociation of the tannin-protein complex occurs rapidly above pH 8 for condensed tannins and above pH 5 for hydrolyzable tannins (Loomis and Battaile 1966; Martin and Martin 1983). Thus high gut pH could conceivably increase the leaf nitrogen available to caterpillars feeding on woody plant foliage.

If this hypothesized mechanism is important in mediating the caterpillar-host tree interaction, trees that have lower leaf pH and/or higher leaf buffer capacity should be less preferred as hosts. Caterpillars would incur greater metabolic costs in maintaining their high gut pH to effectively digest more acidic and/or better buffered leaf tissue and should therefore tend to avoid such host foliage. To test this hypothesis I measured both the pH of freshly homogenized frozen leaf tissue and its buffer capacity as the µmoles NaOH necessary to bring the aqueous homogenate to pH 8.75.

Leaf Phenology

The temporal coordination of herbivore and host life cycles is obviously important, especially in insects like the gypsy moth which break diapause in concert with the emergence of the tree leaves on which they feed. Barbosa et al. (1979) have suggested that differences in tree phenology may influence susceptibility to attack by gypsy moth larvae. To test this hypothesis we made daily observations of canopy development on each tree from which leaves were harvested[4]/. Here the mean of the day a tree's first buds burst and the day 90% of its leaves had expanded was taken as a measure of the timing of its spring canopy formation.

Other Possible Factors

A considerable number of additional factors that might have some influence on gypsy moth host selection were not considered in these initial experiments. In some cases factors were rejected as of little or no importance on the basis of available evidence. Foliage concentrations of P, K, Mg, Na, Al, Ba, Fe, Sr, B, Cu, Zn, or Mn are unrelated to gypsy moth growth and fecundity (Barbosa and Greenblatt 1979; Valentine et al. 1983). Similarly variations in foliage concentrations of 25 amino acids were not correlated with gypsy moth success (Valentine et al. 1983). These investigators do report significant positive regressions of pupal weight on total free sugars and free sugar:Ca ratios; but the ranges in sugar and Ca concentrations sampled were based on both defoliated and undefoliated trees - other factors may well have contributed to these observed correlations. Most earlier reports (Beck and Reese

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[4]/ Lechowicz, M.J. The phenology of leaf emergence in a northern deciduous forest, manuscript in preparation.

1976; Scriber and Slansky 1981) indicated that foliage carbohydrate concentrations are adequate to meet insect requirements. Nonetheless, as discussed subsequently, some carbohydrate fractions may provide token cues important in host selection and, considering the recent results of Valentine et al., the possible importance of carbohydrates in gypsy moth nutrition cannot be dismissed.

Gypsy Moth Host Preferences at Mont St. Hilaires: 1979-1982

The larval host preferences of gypsy moth in the Lake Hill forest were generally stable during the decline of the outbreak in 1979 and 1980 (Fig. 5). *Populus grandidentata*, *Quercus rubra*, *Ostrya virginiana*, *Amelanchier* spp., and *Acer saccharum* were consistently preferred as larval hosts while *Tilia americana*, *Carya cordiformis*, *Prunus pensylvanica*, *Fraxinus americana*, *Acer pensylvanicum*, and *Prunus serotina* were consistently avoided. With the exceptions of *Fagus grandifolia* and *Betula papyrifera*, trees that had erratic electivity values during 1979-80 were poorly replicated in the available samples - *Acer rubrum* or *Juglans cinerea*, for example. The apparent drop in preference for beech in 1980 arises in part from a localized outbreak of nuclear polyhedrosis virus in a single quadrat; the increasing preference for white birch is an interesting but unexplained trend. In general the host preferences during this period of relatively high larval numbers are in accord with the earlier American and European reports reviewed by Lechowicz and Jobin (1983).

In 1981-82 when larval numbers had dropped to innocuous levels, there were some marked shifts in larval preference. Only *Populus grandidentata* was consistently strongly preferred over the 1979-82 interval. *Quercus rubra* and *Ostrya virginiana*, although still preferred, had lower electivity values in 1981 which returned toward their 1979-80 levels in 1982. *Amelanchier* dropped abruptly to being a slightly avoided host and *Acer saccharum* declined steadily to also being avoided in 1982. In contrast *Fagus grandifolia* which had been an avoided host became slightly preferred and *Betula papyrifera* had risen steadily until it was only slightly avoided. Most hosts avoided in 1979-80 such as *Tilia americana* and *Fraxinus americana* were even less preferred by the endemic larval population in 1981-82. There is some indication here that the few most preferred hosts are more heavily used by an endemic population and that the most avoided hosts are especially little used. Intermediate hosts seem to undergo shifts to greater or lesser preference that may potentially be explained by changes in foliage quality. It should be clearly recognized that even at innocuous population levels the gypsy moth population maintains a high degree of polyphagy with virtually all host species attacked to some degree.

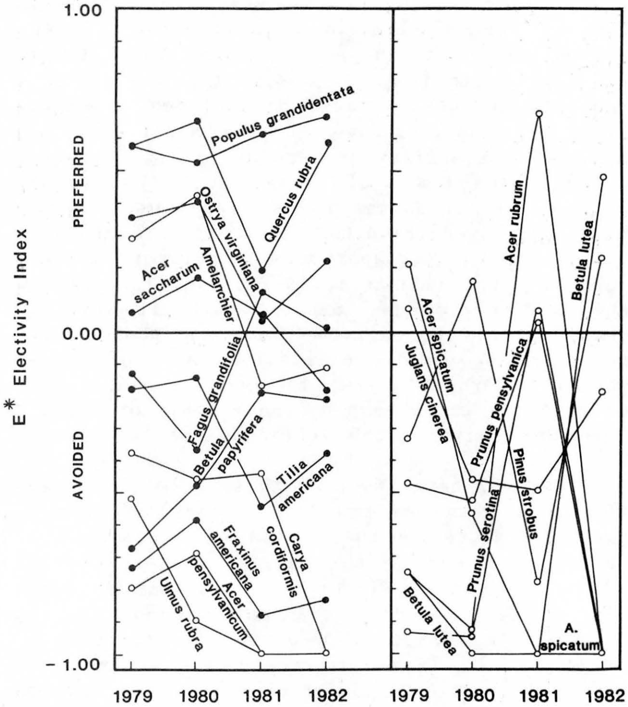

Figure 5. The host preferences of late instar larvae in the Lake Hill forest from 1979 through 1982. The calculations have allowed for occasional missing data; open circles represent electivity values based on fewer than 6 trees. Most of the poorly replicated host species are plotted in the right graph to avoid confounding the interpretation of trends in the generally better replicated species in the left graph.

Because of the inability of female gypsy moth adults to fly and the limited mobility of dispersing larvae (Mason and McManus 1981), these shifts in larval preferences may be explained in part by patterns of egg deposition rather than simply larval dispersal and host selection. It is useful to compare the observed electivities for numbers of egg masses on a host (calculated analogously to that for larvae) to the larval host preferences (Fig. 6). In general more preferred larval hosts also bear a greater proportion of the egg masses in the forest; this is not particularly surprising considering that selection should favor larval preferences for hosts which will allow successful survival and reproduction. It does suggest that late-instar migration to avoided larval hosts for pupation (Rossiter 1980; Mauffette and Lechowicz[5]/) plays only a minor role in the population dynamics of gypsy moth on Lake Hill. On the other hand the cyclic tendencies apparent in the relationships between egg and larval host electivities supports the suggestion that changes in foliage quality may influence larval host preferences. Consider, for example, Quercus rubra which had high larval and egg electivity in 1979; in 1980 larval activity was even slightly higher but egg electivity was sharply reduced. This reduction is reflected in a lowered larval electivity in 1981 but increased egg deposition. In turn by 1982 both larval and egg electivities have returned to 1979 levels. Such cyclic patterns raise the possibility that changes in foliage quality including induced responses such as those shown for birch, oak, and maple (Haukioja and Niemela 1979; Wallner and Walton 1979; Schlicting 1980; Schultz and Baldwin 1980) may influence the gypsy moth population dynamics on host trees from year to year.

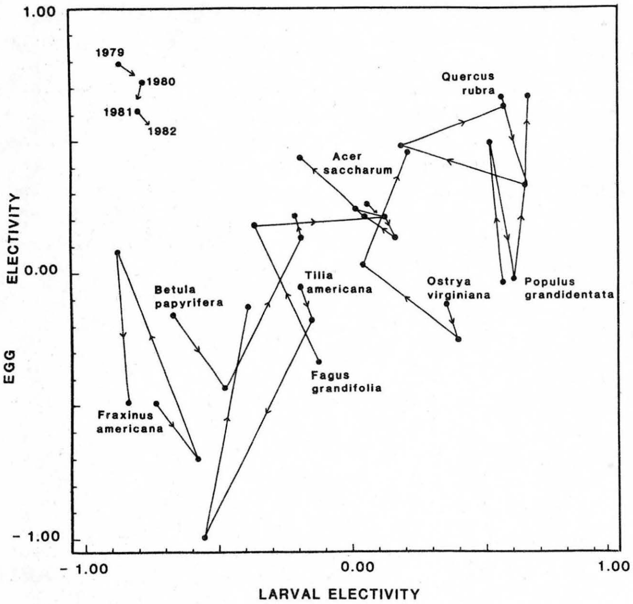

Figure 6. Electivity for egg masses versus that for late-instar larvae in the Lake Hill forest during 1979 through 1982. Trends are shown only for the eight well-replicated host species although all sampled hosts were used to calculate the electivities.

Foliage Characteristics at Mont St. Hilaire: 1979-1982

A multivariate approach to preliminary analyses of the gypsy moth host interaction. It is not possible in this paper to present the detailed results of all the assays of foliage quality in relation to gypsy moth host selection. Instead I have used a multivariate statistical technique that can most concisely be called biplot analysis (Gabriel 1971) to summarize the primary interrelationships between the measured foliage characteristics. Biplot analysis begins with a matrix of rows of objects described by columns of their attributes, in this instance 14 tree species characterized by their mean values for the traits in Table 2. The matrix is first relativized by dividing all entries by the maximum value in their respective columns. The relativized matrix is then centered by subtracting the respective column mean from each entry; this results in comparison of all tree species to a hypothetical, mean tree species. Finally this relativized and centered matrix is analyzed by canonical decomposition, a generalization of singular value decomposition, to acquire the best possible representation in few dimensions of the information in the multidimensional input matrix (see details in Gabriel 1971). The reduced matrix can then be represented graphically in two (hence biplot) or three dimensions to aid interpretation of trends in the data.

In interpreting a biplot such as that of the foliage traits analyzed here (Fig. 7) a number of general rules should be borne in mind. First consider the locations of the individual host species in the two-dimensional graph. Recall that the analysis is centered on a hypothetical mean host plotted at the origin - the dispersion of tree species around the origin is a graph of variation among hosts based on their foliage characteristics. Trees that are closer together are more similar than those further apart on the basis of the foliage traits used in the analysis.

Perhaps the most useful quality of the biplot compared to a technique like principal component analysis (Seal 1964) to which it is closely related is that unlike PCA the biplot also directly illustrates the contributions of individual traits in determining the relationships between trees. For convenience the traits are represented by vectors originating from the origin. The longer a vector, the more variable is that trait among the sampled trees - note however that small differences in a relatively invariant trait may still have important biological effects. The biplot shows only the pattern of variability in traits, the investigator must interpret that variation biologically.

Not only the length but also the direction of the trait vectors in the biplot are important aids to biological interpretation. The cosine of the angle between any two vectors approximates their correlation. Thus acute angles suggest positive correlation and obtuse angles negative correlation; trait vectors at right angles are uncorrelated.

Finally when any vector is extended across the biplot as an axis, the projections of tree species on that axis rank the trees from low to high in regard to that trait in the direction the vector points. In other words the vectors point in the direction that trees with high values of their respective traits will be dis-

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[5] Mauffette, Y. and M. Lechowicz. Utilization of the larval host tree as a pupation site by the gypsy moth, Lymantria dispar L. (Lepidoptera: Lymantriidae), manuscript in review.

placed in the biplot; the actual placement of the tree species arises from the interaction of all the traits which "pull" the species in different directions with different strengths depending on its foliage characteristics.

A cautionary note is in order: like many other multivariate techniques, biplot analysis cannot fully represent all the information in a complex matrix in only a few dimensional graph. The accuracy of the interpretations just described hinges on the amount of variance in the original matrix represented in the biplot. Two vectors apparently highly positively correlated may, for example, actually diverge at a right angle in the third dimension. For this reason biplot analysis can only be an exploratory technique to provide initial help in puzzling out complicated and little known biological situations. It must be supplemented by careful scrutiny of actual correlation coefficients between traits and by traditional graphic comparisons of interrelationships between selected traits. As an exploratory technique biplot analysis can only suggest, not test, hypotheses. Given the large number of interacting traits which may influence gypsy moth host selection it does provide a useful and needed overview which helps focus future research on specific hypotheses involving fewer traits.

Biplot of Foliage Quality

The biplot of foliage traits alone (Fig. 7) emphasizes that many traits implicated in plant defense have fairly stable interrelationships with one another from year to year. For example, the suite of traits involving leaf acidity, buffer capacity, total phenolics, and precipitable tannins is notably stable both in spring and summer and from year to year. Trees with more acidic leaves tend to be consistently higher in total phenolic concentrations. Foliage toughness and water content are generally negatively correlated suggesting that these two traits which have usually been considered separately in the entomological literature may better be combined as a single measure of leaf sclerophylly. Leaf nitrogen concentrations remain relatively stable over time; although the correlations are weak, less sclerophyllous and less acidic leaves tend to be richer in nitrogen. Time of leafing out varies relatively

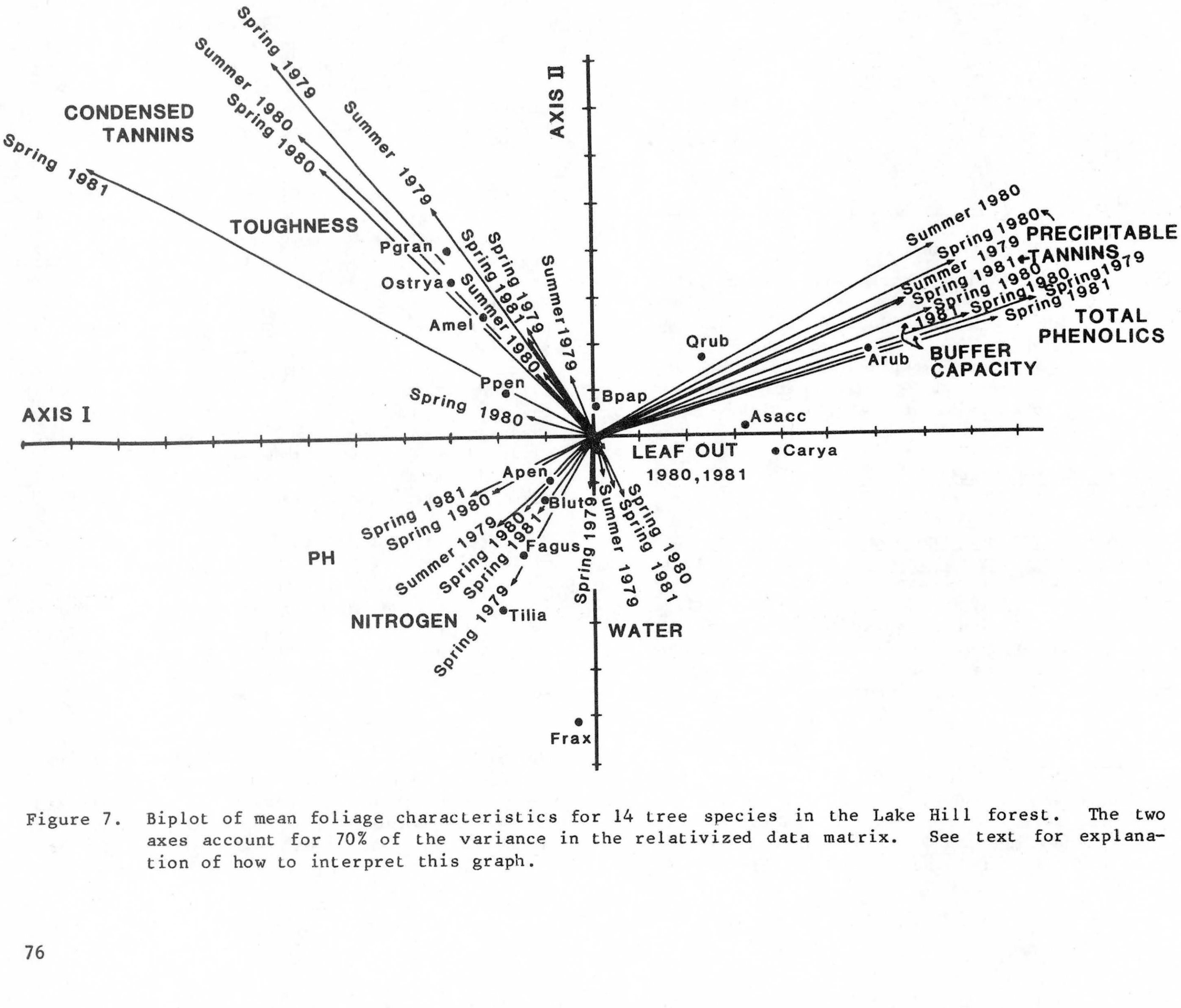

Figure 7. Biplot of mean foliage characteristics for 14 tree species in the Lake Hill forest. The two axes account for 70% of the variance in the relativized data matrix. See text for explanation of how to interpret this graph.

little among the 14 tree species on Lake Hill; actual values have a range of only 8 days in 1980 and 17 in 1981.

The annual pattern in condensed tannin concentrations is in contrast to the generally stable correlations among these other foliage characteristics. Only total phenolics and pricipitable tannins approach condensed tannins in terms of variation between trees. Unlike these other highly variable traits, condensed tannins also showed an interesting pattern of annual variation. During the outbreak year 1979 and 1980 the pattern of condensed tannin levels between tree species was similar and condensed tannins were higher in sclerophyllous leaves (Fig. 7). In 1981 as the gypsy moth population reached innocuous levels there was a shift in this pattern of condensed tannins in the spring leaves of the different host trees.

The host trees themselves fall along two general axes of variation in terms of the traits measured: 1) coordinated variation in a syndrome of traits involving highly intercorrelated changes in acidity, buffer capacity, total phenolics, precipitable tannins, and nitrogen and 2) in another syndrome involving toughness, water content, and condensed tannins. The distribution of tree species in the biplot suggests two relatively distinct modes of leaf phenolic metabolism. Some trees like Populus grandidentata, Ostrya virginiana, and Amelanchier are set apart by their relatively high concentrations of condensed tannins while others like Acer rubrum, A. saccharum, Carya cordiformis, and Quercus rubra have relatively low condensed tannin concentrations but high total phenolics and precipitable tannins. The general validity of these trends and their possible relevance to different modes of defense against folivores merit further consideration.

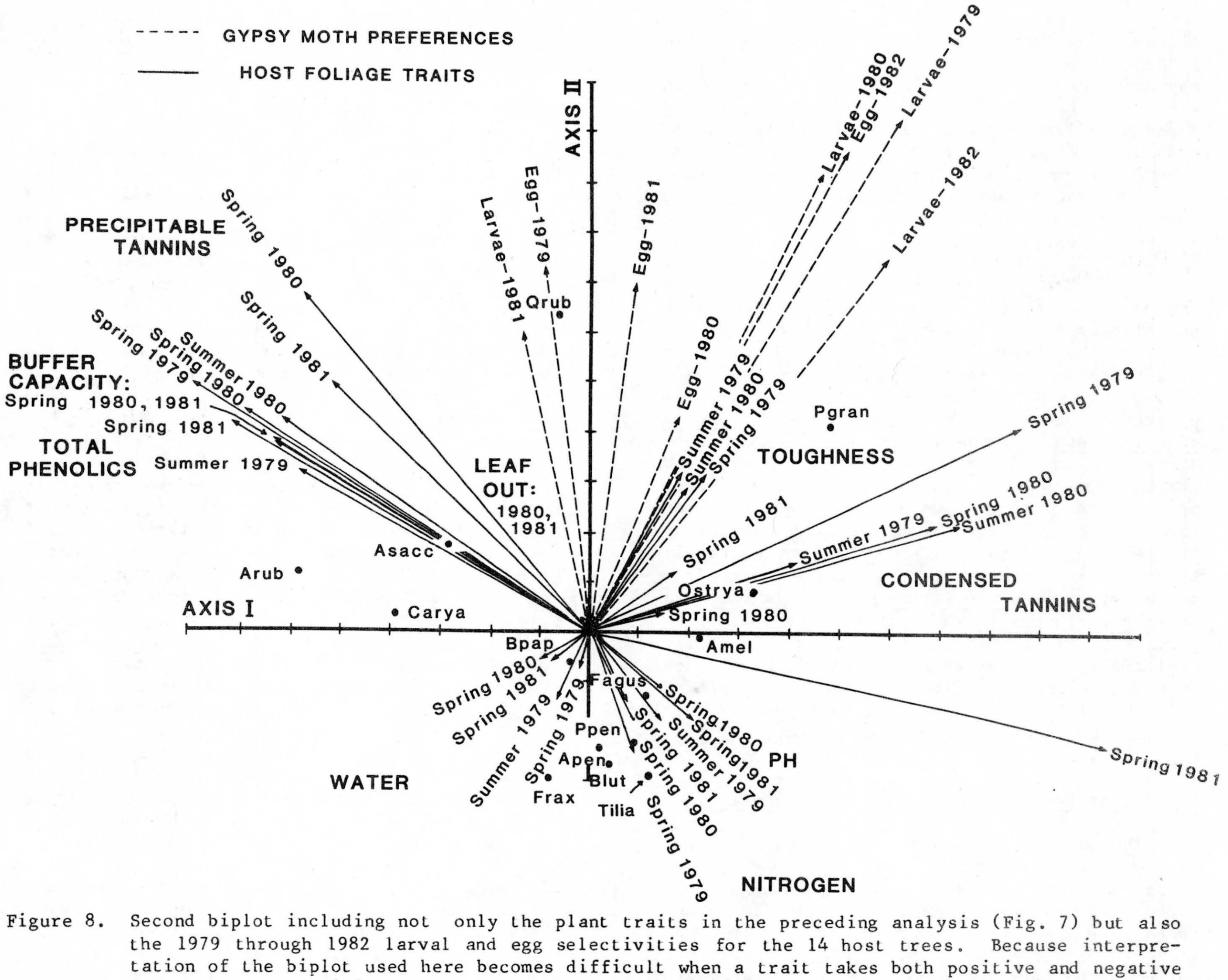

Figure 8. Second biplot including not only the plant traits in the preceding analysis (Fig. 7) but also the 1979 through 1982 larval and egg selectivities for the 14 host trees. Because interpretation of the biplot used here becomes difficult when a trait takes both positive and negative values, the selectivity W rather than the E* electivity values were used in this analysis. Lechowicz (1982) showed that W and E* are very highly correlated. The two axes account for 61% of the variance in the relativized data matrix. See text for further discussion.

Relationships of Gypsy Moth Activity to Foliage Quality

A second biplot (Fig. 8) adding the 1979 through 1982 larval and egg selectivity data for the 14 tree species to that on foliage quality was run to explore the correlations between these plant traits and the patterns of gypsy moth host preference. This biplot retains the underlying relationships of the plant traits among themselves. The two major axes of plant variation involving condensed tannins versus precipitable tannins and total phenolics are still apparent. Precipitable tannins, however, appear to be somewhat more associated with gypsy moth preferences than the other plant traits involved in the same syndrome of variation. Similarly sclerophylly, particularly in the summer, appears more associated with gypsy moth preferences than the concentrations of condensed tannins. Leaf pH, buffer capacity, total phenolics, and nitrogen appear to be only weakly or not at all related to larval host preferences. Although leaf phenology varies relatively little among hosts there is some indication that larvae may prefer hosts that leaf out later. In general this biplot suggests that dispersing gypsy moth larvae prefer trees that later in the season will have tough, dry leaf tissues and that these preferences may be modified in part by leaf concentrations of condensed and, to a lesser degree, precipitable tannins in the spring and early summer.

The actual distribution of host trees in the biplot also indicates that gypsy moth host preferences are not simply and entirely determined by the observed plant traits, but are also influenced by traits not included in this data set. For example, the two most consistently preferred hosts, *Quercus rubra* and *Populus grandidentata*, represent the two different syndromes of leaf types in the biplot of plant traits alone (Fig. 7). It is not immediately apparent what these two hosts have in common that leads to their being attacked preferentially by gypsy moth. *Quercus rubra* in particular is singled out as highly preferred from among trees like *Acer saccharum*, *A. rubrum*, and *Carya cordiformis* to which it is very similar in terms of the observed foliage traits. The biplot (Fig. 8) thus suggests that factors other than those traditionally supposed to determine susceptibility to herbivore attack among trees are important in gypsy moth host selection.

A Model of the Gypsy Moth-Host Tree Interaction

The diverse observational data analyzed here have allowed elimination of certain plant traits as uncorrelated with gypsy moth preferences and therefore unlikely to be important factors in host selection. On the other hand, although no clear and simple explanation of host selection has emerged, certain plant traits are implicated as factors involved in determining the probability that a tree will be attacked by gypsy moth. The recognition of such key traits in this exploratory analysis raises a number of hypotheses which require experimental tests. As a framework for continuing studies I have summarized these hypotheses in a tentative model of gypsy moth host selection which is explained below. The model has two main tenets: 1) that dispersing gypsy moth larvae preferentially settle on trees with higher sugar:tannin ratios in their young foliage and 2) that stress-induced variations in the sugar and tannin concentrations of young foliage can lead to year to year variation in a tree's susceptibility to attack by gypsy moth.

On a regional basis, the forests most susceptible to infestation by gypsy moth occur on more arid, nutrient-poor sites (Houston and Valentine 1977) where sclerophyllous tree species are most frequently found. Within these susceptible forests, host trees with more sclerophyllous mature foliage appear from the present analysis to be preferentially attacked by gypsy moth larvae. This positive association between sclerophylly and the host preferences of gypsy moth provides a useful clue to the possible basis of host selection by this polyphagous folivore.

Sclerophylly has long been associated with both arid, nutrient-poor environments and low rates of carbon fixation (Small 1973; Seddon 1974). Sclerophylly is believed to improve survival during the relatively frequent periods of stress typical of such habitats but at the expense of reduced productivity when conditions are favorable. In general we might expect the less productive sclerophyllous tree species to have more limited resources to allocate to defenses against folivores. In addition the leaves of sclerophyllous trees tend to develop more slowly in the spring (Federer 1976). Thus gypsy moth larvae feeding on the spring and early summer foliage of a sclerophyllous host may enjoy a relatively longer period of access to higher quality, immature foliage; models of gypsy moth larval development (Valentine and Talerico 1980) suggest that selection of hosts offering even slightly longer periods of favorable foliage availability can improve larval survival and fecundity. Host trees that later in the summer are most sclerophyllous and then apparently lowest in foliage quality may actually have provided the longest periods of immature foliage most favorable for larval development.

How then might dispersing larvae recognize the sclerophyllous hosts offering such a favorable opportunity for larval development? During larval dispersal all the available foliage is relatively tender and moist and there are no consistent correlations between the sclerophylly of young and old foliage; some cue other than sclerophylly itself must be used by the dispersing larvae. Soluble sugars, especially sucrose, which are known to be an important feeding stimulus in very many insects (Dethier 1982) seem the most likely proximate control on host selection by dispersing gypsy moth larvae. Transport of soluble sugars to developing tree leaves is high (Dickson and Larson 1981) and would continue longer in the more slowly developing sclerophyllous species. Depending in part on the relative timing of eclosion and bud break, dispersing larvae will thus be more likely to encounter sugar-rich foliage on the slower-developing, sclerophyllous hosts. Further study is necessary to test this hypothesis that soluble sugar concentrations in host foliage during dispersal actually determine host selection.

Further investigations should also consider the possible interaction between soluble sugar and tannin concentrations. Dethier (1982) has reported that although gypsy moth larvae cannot sense tannic acid per se, this hydrolyzable tannin does suppress the larvae's electrophysiological response to sugars. Perhaps tannins alter the apparent levels of soluble sugars in the young foliage available to dispersing larvae. If this is the case we may hypothesize that gypsy moth preferentially attack trees that have high sugar:tannin ratios in their young foliage.

Tannins present in young foliage during larval development may also influence year to year trends in the numbers of dispersing larvae that potentially settle on different host trees. Because of the limited vagility of the later instars and female adults of the gypsy moth (Doane and McManus 1981; Wallner, this volume), any reduction in foliage quality on attacked trees will act to limit larval success on that tree and thereby reduce the local density of dispersing larvae the next year. Data for lepidopteran larvae including the gypsy moth (Feeny 1968; Karasov and Satarova 1973) have shown that tannins can reduce foliage digestibility. High tannin levels in the young foliage critical for larval development can thus reduce egg deposition by female larvae on these hosts. If in addition elevated levels of tannins can be maintained in young foliage the next spring, then the preference of dispersing larvae for the host may be further reduced by suppression of the neurophysiological response to sugar stimuli as hypothesized above. The maintenance of high tannin levels, however, depends on the availability of photosynthetic reserves which will tend to be lower in more sclerophyllous hosts. Sclerophyllous hosts will therefore tend to be more susceptible to sustained infestations of gypsy moth larvae from year to year. Moreover, productive hosts better able to either constitutively or facultatively maintain high levels of tannins in their spring foliage could actually shift large numbers of dispersing larvae to the less well-defended, sclerophyllous hosts. It is through mechanisms such as these that the gypsy moth preference for more sclerophyllous hosts may be expressed and maintained.

This model is in accord with the recent revival and elaboration (Haukioja 1980) of the idea that climatic stress on host plants can release a serious outbreak of insect herbivores. When all trees have been weakened by a stress such as a severe drought, limited reserves of photosynthate may be diverted from defense to other more essential functions. The polyphagous and widely dispersed gypsy moth larvae in the subsequent spring then would find an unusually high number of favorable host trees apparently high in sugar content for lack of masking tannins. Larval success on these drought stressed trees would be relatively high and defoliation would thus reduce the recovery of photosynthate resources even if climatic conditions were again favorable. Gradually enhanced defenses, probably aided by predator and pathogen attacks on gypsy moth (Doane and McManus 1981), would reduce the larval numbers to low enough levels for the normal patterns of leaf development and defense to prevail. The endemic gypsy moth population then would again preferentially attack the more sclerophyllous hosts which are generally less able to maintain effective tannin-based defenses and have the longer leaf development times favorable to gypsy moth larval success.

The model proposed here can potentially explain two key aspects of the gypsy moth-host interaction: 1) the basis of host selection and 2) the occurrence of periodic outbreaks. Additional observational and experimental tests are necessary to test its validity.

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CHANGES IN TREE QUALITY IN RESPONSE TO DEFOLIATION

Jack C. Schultz[1] and Ian T. Baldwin[1]

Research Assistant Professor and
Senior Research Assistant
Department of Biological Sciences
Dartmouth College, Hanover, NH 03755

Abstract

Plant chemistry alone fails to explain why most trees escape defoliation most of the time. Chemical variation in space and time, acting to enhance the effectiveness of natural enemies, may be the key. Changes and increasing variation in direct response to insect attack ("induction") may be particularly important for irruptive pests.

Introduction

The search for an explanation for pest outbreaks and cycles has long been a focus of CANUSA and represents a multimillion dollar question. It is interesting to consider, however, that such outbreaks are actually rare. Few insect species exhibit them, and they are widely scattered in time (Schultz 1983a). Most insect species do not exhibit irruptive population dynamics, and exist at very low abundances almost all the time (Lawton and McNeil 1979). The occurrence of irruptions leads one to suspect that some regulatory factor has failed or been defeated. Since many things kill herbivorous insects and/or influence their feeding, growth, and fecundity, there is no shortage of possible explanations. Nonetheless, no successful generalization has emerged about these events; instead, individual investigators favor individual hypotheses (Schultz 1983a).

In our laboratory we emphasize the influence of host tree quality, especially defensive chemistry, on the performance of defoliating insects. The reason for this is that among those factors likely to be important to the insect, food quality is one which may influence all others, including the effectiveness of parasites, pathogens, and predators (Lawton and McNeil 1979, Schultz 1983a). Our major working hypothesis has two main parts: 1) tree chemistry has an impact on defoliating insects, but chemical variability is the key, and 2) the importance of host chemistry derives from its interaction with other mortality and morbidity factors.

The reason for following this line of reasoning involves the observation that the relationship between insect and host plant is coevolutionary in nature (Ehrlich and Raven 1965). Each participant exerts natural selection on the other, resulting in an escalating "arms race". On the plant's part, chemicals may be produced which function as defenses against insects (Ehrlich and Raven 1965, Feeny 1970, Swain 1979). However, the presence of these chemicals selects for the ability to detoxify or avoid them on the part of the insect (e.g. Brattston 1979). If any plant or plant species were to defend itself with a uniform, singular chemical defense effective enough to keep insects as rare as they are most of the time, we would expect this strong selection to favor the evolution of insects immune to it (Maiorana 1981, Schultz 1983a). Exactly this result is common in agricultural systems, where humans apply the defense as artificial (or plant-derived) chemicals, or employ uniform, resistant cultivars (Lupton 1977). Since forest trees live many years (and many insect generations), something else must be important in defending them, because "super pests" do not continuously defoliate forests. We argue that "something else" necessarily involves variable plant chemistry.

Induced Variability

A form of variation we have been studying lately involves damage-induced changes in leaf chemistry in forest trees. A decrease in food value or increase in the concentrations of antiherbivore chemicals has now been observed in black oak (Wallner and Walton 1979), red oak (Schultz and Baldwin 1982), red alder and willows (Rhoades 1982), arctic birches (Haukioja and Niemela 1978, Bryant 1981), yellow birch, sugar maple, and poplars (Baldwin and Schultz 1983 and unpublished), to mention a few. It is becoming clear that tree leaf quality varies not only in space (e.g., Schultz et al. 1981, Whitham 1981, Zucker 1982) and seasonally (Feeny 1970, Schultz et al. 1981), but also rapidly in response to attack. We have found, for example, that phenolic concentrations are increased as much as 150% in undamaged leaves of partially (10%) defoliated sugar maples and poplars within 36 hours, apparently through de novo synthesis (Baldwin and Schultz 1983).

The potential significance of this form of leaf quality variability for understanding pest outbreaks takes several forms. First, the ongoing decline in food quality that results may help explain the conspicuous decline in insect population "quality" which occurs during irruptive episodes, including slowed caterpillar growth, reduced maximum size, and lowered fecundity (Wellington 1965, Wallner and Walton 1979, Rhoades 1979, Schultz and Baldwin 1982). Such declines often occur before available food is depleted, suggesting possible food quality reduction. Low food quality under induction alternating with high food quality under "relaxation" (and especially during periods of plant stress) might generate the cyclic behavior some pest populations exhibit (Haukioja and Hakala 1975, Bryant 1981).

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[1] Present address: Department of Entomology, Pennsylvania State University, University Park, PA, 16802.

Second, increased effectiveness of predators, pathogens, and parasites as irruptions proceed could be due to or augmented by declining host plant quality (Schultz 1982). An estimated 26% increase in gypsy moth mortality due to tachinid fly infestation could result from the 3-4% reduction in caterpillar growth rates on "induced" foliage (Schultz 1983a). If lowered food quality influences searching behavior by larvae, so that more movement and tasting occur, contact rates with pathogens should increase (Schultz 1983a,b). Preliminary results in our laboratory suggest that gypsy moth larvae fed protein-deficient diets do indeed exhibit increased movement and searching behavior (Schultz, unpub. data).

A third potential consequence of the induction effect involves the role of spatial variability. More detailed chemical comparisons of oak leaves taken from trees being defoliated by gypsy moth larvae with those from unattacked trees growing nearby (see Schultz and Baldwin 1982 for sampling, extraction, and site descriptions) reveal differences in variability as well as total amounts of some phenolic compounds. Using capillary GLC methods for the quantitative analysis of two hydrolyzible tannins, gallic acid and ellagic acid (Arpino et al. 1977, Baldwin in prep.), we may plot the frequency distributions of leaves having various dry weight concentrations of these two astringent compounds. When we do this (Fig. 1), we find that undamaged leaves on "induced" trees exhibit significantly different frequency distributions (Chi^2 test, $p < .05$). Leaves from damaged trees have a significantly wider range of values than do leaves from unattacked trees.

Any insect which can perceive these chemical differences has a wider range of leaf values from which to select a preferred type. In an induced tree, fewer leaves fall into the lower hydrolyzible tannin content classes; hence an insect responding to gallic and ellagic acids as antifeedants must search farther and longer for suitable leaves. This could increase metabolic travelling costs, search time per consumption time, contact rates with pathogens and predators, and conspicuousness to predators and parasites (Schultz 1983a,b). Increased variability, together with overall lower leaf quality, should increase a variety of risks.

Some insects may not discriminate among leaves, but eat the broader range found in induced trees. Recent evidence suggests that switching from high to low quality or low to high quality leaves can result in even poorer growth performance than is attained on a diet consisting of only poor quality leaves (E. Haukioja, unpub. data). In either case, induced trees which also exhibit increased variance could become much poorer hosts than they were before they were attacked.

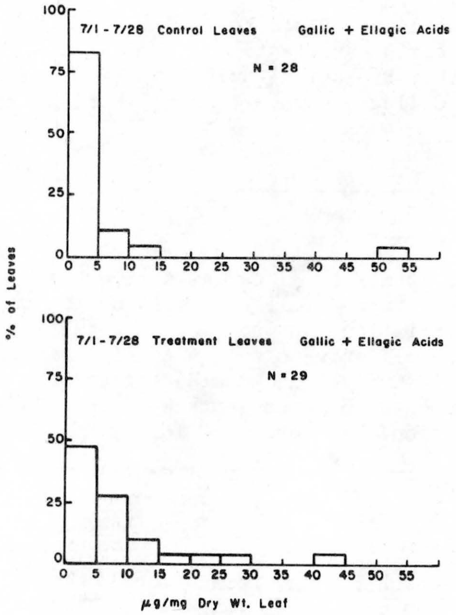

Figure 1. Frequency distributions of hydrolyzible tannin contents of leaves from red oak trees undamaged by gypsy moth larvae (top) and undamaged leaves from nearby trees defoliated 80-100% (bottom) during 1981.

Because the secondary chemistry of forest trees is often dominated by phenolics, especially tannins (Swain 1979), these are the compounds most studied in the context of induction. Recently, the importance of their biological activity as antiherbivore devices has been called into question (e.g., Bernays 1978, Martin and Martin 1983). Several investigators have found weak or nonexistent correlations between tannin contents and insect performance (e.g., Mattson, this volume, Wagner, this volume). There are at least two possible reasons for this. First, sampling for phenolics is made very difficult by the observation that tissue-to-tissue, leaf-to-leaf, and needle-to-needle variation is so great (Schultz et al. 1981). This means that we must know the phenolic/tannin content of the tissue actually consumed; it is not sufficient to sample similar, or even nearby tissues for correlative studies. The adjacent leaf may not represent or even resemble the chemical composition of the leaf an insect consumed. Second, both sampling and consumption can alter tissue chemistry. Hence, we have a catch-22: we must know what the chemical composition of a plant tissue was when the insect began to feed on it, but once the insect feeds on it, any remaining portion may be altered. In nature, insects may select low-phenolic tissues, but once partially eaten, our sampling and analysis may show them to be high-phenolic tissues.

Conclusions

This last point brings us to a point which is critical for understanding the role of tissue chemistry in the interaction between tree and insect. This observation is simply that because tissues vary tremendously in space and time, insects have a choice in selecting food. They may avoid tissues with one type of composition while seeking out tissues with other compositions, to which the insect may be physiologically adapted. As a result, understanding insect behavior and its sensory and ecological bases is central to explaining why certain insects eat certain tree species, move among individual trees, grow and reproduce better on some trees than others or at some times than others, or are more susceptible to natural enemies at certain times or in certain places. These issues, of course, are fundamental to answering the questions about population dynamics that interest us all. It is clear that studies of insect behavior, tree quality and tree chemistry are needed to understand insect population dynamics, but that we must pay as much attention to variances as to mean values.

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EFFECT OF FERTILIZATION ON WESTERN SPRUCE BUDWORM FEEDING IN YOUNG WESTERN LARCH STANDS

Wyman C. Schmidt[1] and David G. Fellin[2]

[1]Research Silviculturist and Project Leader, USDA Forest Service, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717

[2]Supervisory Research Entomologist, USDA Forest Service, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Drawer G, Missoula, MT 59806

This study evaluated effects of fertilization of young western larch stands on western spruce budworm feeding in Montana. Various combinations of nitrogen, phosphorus, and potassium resulted in nearly double the amount of feeding by western spruce budworm larvae, with nitrogen eliciting the most response. Larch growth response to fertilization can be negated by increases in budworm feeding.

Introduction

Forest fertilization is relatively new to the Northern Rockies and is primarily limited to experimental areas. Western spruce budworm (*Choristoneura occidentalis* Freeman), a defoliating insect native to the Northern Rockies, has persisted in epidemic proportions since the late 1940's. Although reported long before that, it was not considered a serious threat to forest management until about 1950. In the early 60's, we discovered and described the feeding behavior of western spruce budworm on young western larch (*Larix occidentalis* Nutt.) (Fellin and Schmidt 1967). Instead of foliage feeding only, budworm were found feeding on and severing the stems of new shoots of larch, jeopardizing the straight form and rapid juvenile height growth characteristic of this species. Subsequent evaluations of this unusual feeding habit showed that indeed height growth was reduced about 25 to 30 percent by these terminal and upper lateral stem severances and that there was at least a temporary reduction in form quality (Schmidt and Fellin 1973; Fellin and Schmidt 1973a).

Silvicultural attempts at dealing with forest pest problems have a long history, particularly with some of the beetles. One of these cultural methods--fertilization--has had only limited evaluation. In a review, Mustanoja and Leaf (1965) noted that "fertilizers have differential effects on insects, the effects being more or less similar within certain genetic groups." They note, however, that "the populations and attacks of all studied species of macrolepidoptera . . .," of which they list four, " . . . have been reduced with mineral fertilizers (especially N) and lime." They attribute the effect to increased larval mortality. In another review, Stark (1965) lists 28 fertilizer trials involving about a dozen species of forest insects in as many genera. In 21 of these trials, the treatment adversely affected the insects--including sawflies, shoot moths, aphids, and caterpillars--as reflected in reduction of cocoon or pupal density, increased larval mortality, decrease in female weight, and so forth. Six of the 28 trials showed no fertilizer effect and one showed increase in insect feeding.

In some specific examples, Merker (1958, 1961, 1963), studying 20- to 50-year-old spruce infested with *Pristiphora abietina*, found that he could significantly reduce pupal density and injury to shoots, sometimes in the same season, by applying NH_4NO_3, $CaCO_3$, or urea. Also, nitrogen applied as part of an NPK treatment to eastern white pine resulted in the least amount of damage by the white pine weevil, *Pissodes strobi* Peck, but the nitrogen treatment also resulted in the shortest trees (Xydias and Leaf 1964).

Conversely, there are documented cases where fertilizer increased the number of insects and/or stimulated feeding. For example, Xydias and Leaf (1964) found the greatest incidence of attack by the white pine weevil occurred with the same treatment of potash that resulted in the tallest trees. The treatment apparently made trees more palatable to the weevil. Also, Carrow (1967) found that the establishment rate of balsam woolly aphids (*Adelges picea* [Ratz.]) on Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) grown on a humic, nitrogen-rich soil was 2.5 times as high as on host trees grown on a mineral nitrogen-poor soil. Increased pupal weights of spruce budworm (*Christonerua fumiferana* Clem.) were found on nitrogen fertilized balsam fir (*Abies balsamea* [L.] Mill.). These increased pupal weights were in turn positively correlated with increased numbers of larvae produced per female moth (Shaw and others 1978). Hughes and Jackson (1962) found fertilizer mixtures of either N, P_2O_5, or K_2O at the 100-lb/acre (112-k/ha) rate resulted in a highly significant increase in the incidence of attacks by a phloem insect, *Dioryctria amatella* (Hulst), to slash pine (*Pinus elliottii* Engelm. var. *elliottii*). Of the three components, incidence of attack was most closely associated with mixtures containing phosphorus. Even at the 50-lb/acre (56-k/ha) rate, phosphate in mixed fertilizers increased insect attacks fourfold over treatments containing no phosphate.

Soil type and/or host tree condition may be influential in the effect of some fertilizers on forest insects. In Sweden, poorly growing pine trees treated with phosphorus or nitrogen were little affected by attacks of the European pine shoot moth (*Rhyacionia buoliana* [Schiff.]). However, healthier trees treated with fertilizers affording phosphorus or nitrogen suffered heavy damage by the shoot moth (Eidmann and Ingestad 1963). Hughes and Jackson (1962) found *Dioryctria amatella* (Hulst) injury to slash pine most prevalent among fast growing trees; damage was negligible among slow growing trees of the same size in an adjoining plantation.

Insect predator-host relationships may also be involved in fertilizer responses. Thalenhorst (1964) warns against premature assumptions about the effects of fertilizers on insects. He describes a fertilizer trial in a spruce plantation where aphid species, mostly *Cinaropsis pilicornis*, infestations in May were heaviest on NPK and slightest on PK plots. However, since predator populations, particularly a lady beetle, *Coccinella septempunctata*, were also most numerous on these densely populated plots, the position was completely reversed a month later.

No general agreement exists on the mode of action in fertilizer interactions with insects. The physiology of the tree may be involved. Mustanoja and Leaf (1965) note that with some insects the sugar:protein ratio of the needles is important for nutrition of the larvae, and anything that decreases this ratio--water or mineral fertilizers, especially nitrogen--increases larval mortality. Carrow (1967) noted that an amino acid imbalance in the bark tissue of host trees was induced by fertilization with NH_4NO_3 and may have been responsible for a population decline of aphids. Also, nutrients may produce structural changes in host plant tissues that affect insect feeding. Lignification of plant tissues (Mustanoja and Leaf 1965), size of food (finely comminuted versus whole needles) (Merker 1961), and coarser bud scales or greater resin flow (Oldiges 1959) are all cited as possible effects of nutrient fertilization that in turn affected the feeding behavior of insects on the host trees.

Another hypothesis is that fertilizer elements are incorporated directly into various insect tissues, often with fatal or deleterious effects. Merker (1962) notes that the direct effects of absorbed fertilizers on forest pests are much more severe than any indirect effect upon the physiological condition of the tree. However, Carrow and Graham (1968) imply that treatment of host trees with ammonium nitrate reduces populations of the balsam woolly aphid primarily by inhibiting initial settling of larvae on the host trees.

Although there is apparently little consistency in the results of fertilizer trials--due in part at least to questionable observations on small plots, lack of knowledge of the nutritional and moisture relations of the soils, or impracticable methods--there does appear to be general agreement that fertilization affects the behavior of many insect populations (Stark 1965).

Neither the technical or economic aspects of forest fertilization are well understood, particularly in the Northern Rockies. Nevertheless, it is important that tree response to fertilization and interactions with other factors in the ecosystem be evaluated. With this in mind, we undertook the subject of this paper--the interaction of western spruce budworm with different combinations of fertilizers in young western larch forests of western Montana. This is the first report of the results of this exploratory study.

Methods

This western spruce budworm study was superimposed on a conventional fertilizer study that aimed primarily at determining the effect of different combinations of fertilizer on growth of young western larch forests. The original fertilizer/growth study established in 1966 consisted of 175 experimental plots at 13 locations in western Montana (Behan 1968). The basic design of the original fertilizer/growth study was a randomized block of six treatments replicated three times at each location. However, because of limited area or lack of sufficient homogeneity of the stands, it was not always possible to apply all six treatments. Hence, at each location, there were from two to six treatments, including controls of no fertilizer, but always three replications.

The fertilizer/budworm study reported here was established 2 years later in 1968 and was limited to four of the 13 locations of the original fertilizer/growth study. All four locations were within the budworm-infested areas of the Lolo and Flathead National Forests. The treatment combinations on these four plots are shown in Table 1, where the control had no fertilizer and the treatments were composed of various combinations of nitrogen, phosphorous, and potassium.

Table 1. Description of site, stand, and treatments used for this larch fertilizer/western spruce budworm study.

		Stand condition at time of treatment			
Location	Age	Height (feet)	Average density (trees/acre)	Site index (50 yr)	Treatments
Upper Cottonwood	12	6 to 12	7,000	60	Control, NPK
Lower Cottonwood	12	4 to 8	300[a]	65	Control, NPK, N, NK, NP, PK
Rice Ridge	18	5 to 15	3,500	70	Control, NPK, N, NK, NP, PK
Barber Creek	11	4 to 10	3,600	80	Control, NPK, N

[a] thinned.

Nitrogen (N) was in the form of urea at the rate of 300 lb/acre (336 k/ha), phosphorus (P) was treble superphosphate at the rate of 200 lb/acre (224 k/ha) of P_2O_5 (phosphorus pentoxide), and potassium (K) was potassium chloride at the equivalent of 200 lb/acre (224 k/ha) of K_2O (potassium oxide). For example, the NPK treatment consisted of 300 lb nitrogen, 200 lb phosphorus, and 200 lb potassium per acre. Fertilizers were preweighed and applied separately with a hand spreader on the plots.

To sample the interaction of the budworm and the fertilizer treatments, five of the tallest trees per plot were randomly selected. Each tree was stratified vertically into six strata. In each stratum, beginning with the topmost stratum, we selected a branch or branches and examined the first 100 fascicles, beginning distally on the branch. Branches selected were in a helical pattern moving down the tree; i.e., the first branch selected on the south side of the tree, the next on the southwest, the next on the west, and so forth. Each branch was tagged for initial and subsequent measurements. On these 100 fascicles, we determined the number of larvae and the number of fascicles damaged during the larval feeding period. After the larval feeding was completed, we examined the same 100 fascicles to determine the number of damaged fascicles. Larvae counts were made the second year after fertilization on all four study areas. Observations, but no larval counts, were made in measurement years four and six.

In addition, on these same branches in each stratum, we determined the larval damage done to the lateral shoots in four categories: (a) no feeding; (b) needle feeding only; (c) external mining of the shoot; and (d) shoot severed (fig. 1). Damage to the terminal shoot of each tree was evaluated and classified into the same four damage categories listed for the lateral shoots.

Measurements of injuries caused by western spruce budworm larvae were taken in 1968, 1970, and 1972--2, 4, and 6 years after the fertilizers were applied in fall of 1966.

Results

Western spruce budworm larvae fed on the young western larch trees on these fertilizer study plots in much the same manner we described earlier (Fellin and Schmidt 1967, 1973a; Schmidt and Fellin 1973). However, budworm fed more heavily on larch in the fertilized plots than they did in the control plots. Overall, the effects of fertilizer treatment on budworm feeding were essentially the same on all four study areas. The absolute amount of budworm damage varied by area because of difference in budworm populations, but the ratios of larval damage in the fertilized and control plots were much the same. The following sections describe the types and amounts of budworm feeding as related to fertilizer treatment.

Fascicle Damage

The first noticeable budworm damage to larch in the spring was from larvae feeding on the larch fascicles. Fascicle needles started emerging in late March, well before the terminal and lateral shoots started to elongate (Schmidt and Lotan 1980). Thus, the fascicle needles were the first readily available source of foliage for the budworm on young larch.

Budworm fed on fascicles about one and a half to twice as much on the fertilized plots as they did on the control (not fertilized) plots (Table 2). This was particularly apparent on any of the plots where nitrogen was at least one of the components of the fertilizer treatment. Effects of PK treatment on budworm feeding were far less pronounced than those treatments that included nitrogen, but damage on the PK treatment exceeded that on the control plots.

Table 2. Percent fascicles injured by western spruce budworm larvae 2 years after fertilization.

Treatment	Lower Cottonwood	Upper Cottonwood	Rice Ridge	Barber
	- - - - - - -	(percent)	- - - - - - -	
NP	25	--	28	--
N	28	--	23	3
NK	22	--	26	--
Control	12	6	13	2
PK	14	--	18	--
NPK	20	15	21	2

Larvae fed on fascicles throughout the crown but fed more heavily on those in upper strata of the live tree crowns (Fig. 2). The number of fascicles fed on was about three times heavier in the upper crown than in the lower crown. This is consistent with observations we had made earlier of budworm feeding behavior (Schmidt and Fellin 1973).

Lateral Shoot Damage

Budworm larvae severed about one and a half to twice as many of the succulent new shoots of lateral branches on fertilized plots as on the control plots (Table 3). Over half of the lateral shoots were severed by budworm larvae on the fertilizer plots at Rice Ridge the second year after fertilization compared to about one-fourth of the lateral shoots on the control trees. Like fascicle feeding, the PK treatment results fell intermediate between those treatments that included nitrogen and the control. Since the above injuries coincided with a generally heavy budworm infestation in the area, practically none of the trees escaped some type of budworm feeding, even those on the control plots. Only 8 percent of the trees in the control plots weren't fed on in some manner.

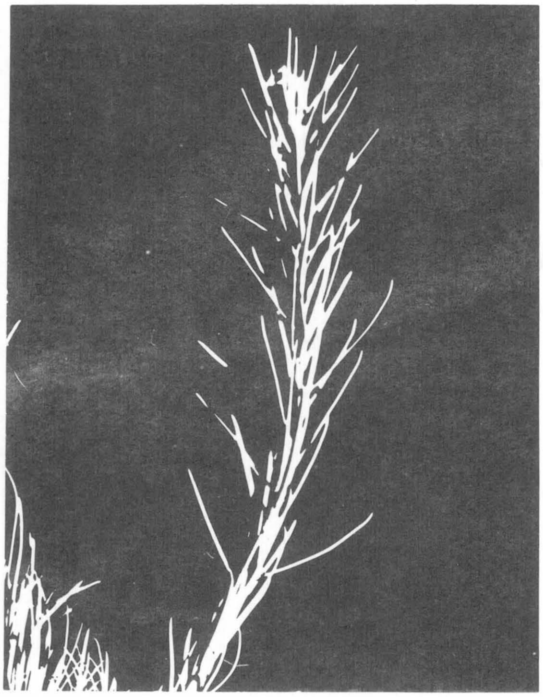

Figure 1a. Types of western spruce budworm feeding on western larch--no feeding.

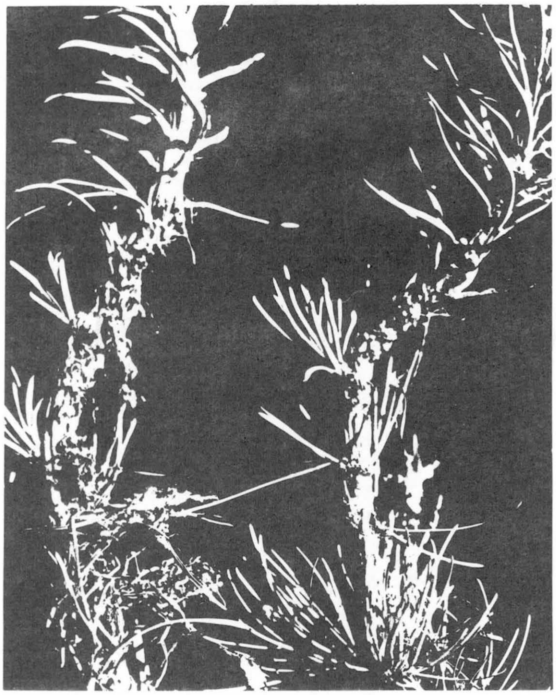

Figure 1c. Types of western spruce budworm feeding on western larch--external mining of the shoot.

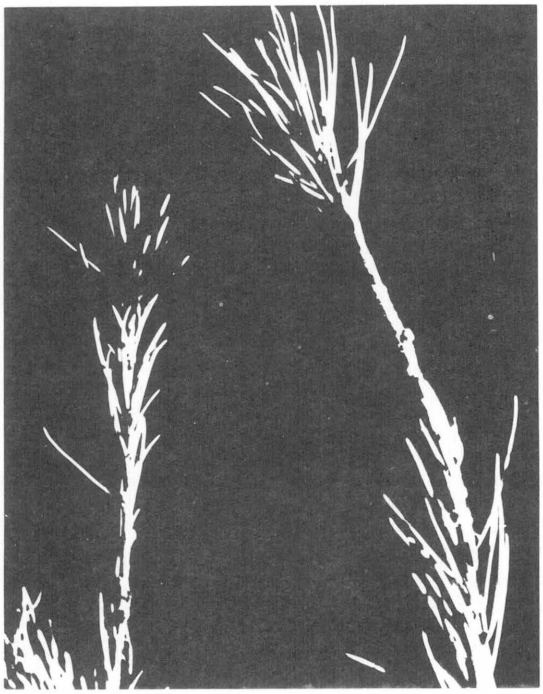

Figure 1b. Types of western spruce budworm feeding on western larch--needle feeding only.

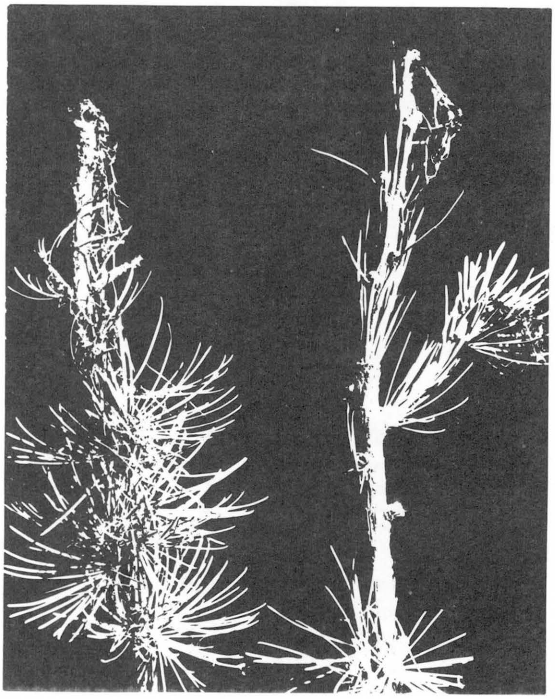

Figure 1d. Types of western spruce budworm feeding on western larch--shoot severed.

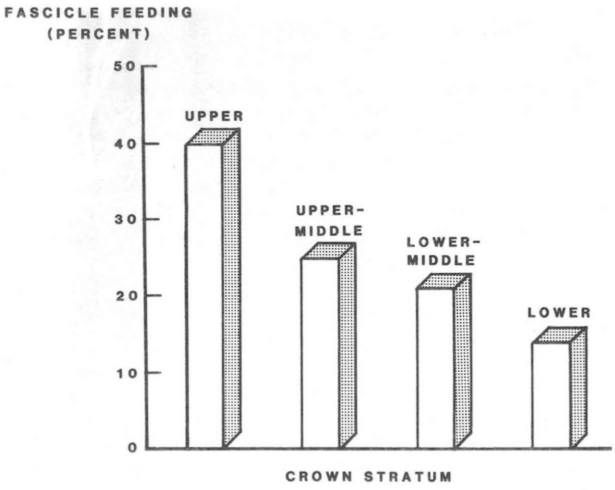

Figure 2. The percent of fascicles fed on by western spruce budworm larvae at four crown levels 2 years after fertilization (Lower Cottonwood). This includes only the upper four of the six crown strata. The lower two strata were in the receding portion of this shade-intolerant species and showed practically no budworm feeding.

Table 3. Percent lateral shoots of western larch severed by western spruce budworm at Rice Ridge and Lower Cottonwood 2 years after fertilization.

	Type of damage			
	Rice Ridge		Lower Cottonwood	
Treatment	None	Lateral shoots severed	None	Lateral shoots severed
	(percent)			
NP	1	56	10	65
N	1	53	6	68
NK	1	52	5	65
Control	8	23	21	34
PK	2	44	25	37
NPK	1	54	10	58

We see little difference in percent lateral shoots severed between those four treatments that included nitrogen (Fig. 3). Budworm severed about twice as many of the lateral shoots on the nitrogen treated plots as on the controls. Lateral shoot severance ratios on the PK treated plots were intermediate to the controls and the plots with nitrogen.

The effect of fertilization on lateral shoot severance by western spruce budworm larvae was relatively consistent from area to area. The absolute amount of damage varied by area because of differences in budworm populations, but the ratios of damage on the NPK and control plots were much the same (Table 4). Lateral shoot severances were about one and a half to twice as great on NPK plots as on the controls.

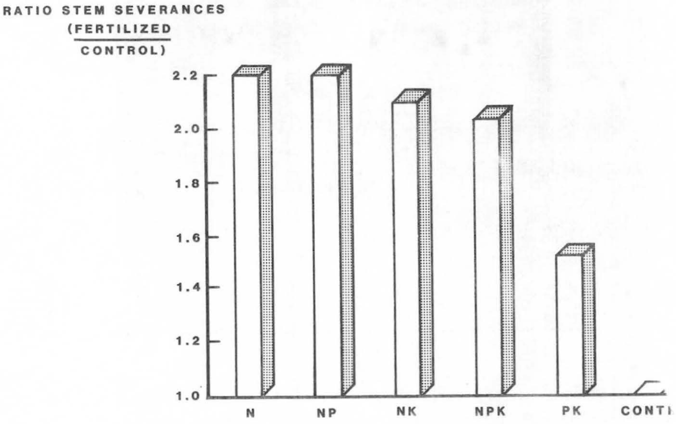

Figure 3. Budworm severance ratios on fertilized and control plots (fertilized/control) at Lower Cottonwood and Rice Ridge 2 years after fertilization.

Table 4. Effect of NPK fertilizer on the percent of lateral shoots severed by western spruce budworm larvae on four study areas two years after fertilization.

Damage	Area	Control	NPK[a]
		--(percent)--	
Shoots severed	Lower Cottonwood	36	54
	Upper Cottonwood	34	58
	Rice Ridge	39	67
	Barber	7	10
None	Lower Cottonwood	21	10
	Upper Cottonwood	28	14
	Rice Ridge	1	1
	Barber	84	82

[a] The NPK and control treatments were the only treatments common to all four study areas.

The effect of budworm larval populations is most readily detected in the trees that had no damage (Table 4). For example, Rice Ridge had a high budworm population 2 years after fertilization and only 1 percent of the lateral shoots escaped both needle feeding and severance in both the NPK and control plots. Meanwhile, on the Barber area where budworm populations were light, over 80 percent escaped all types of damage.

Fertilization effects on budworm feeding, particularly in the most severe form of feeding (shoot severance), diminished rapidly (Table 5). The largest absolute differences in budworm feeding by fertilizer treatments occurred the second year after fertilization. This coincided with the year of greatest tree diameter growth response to fertilization (personal communication with Dr. Mark Behan, University of Montana, Missoula, 1982). Evaluations to determine treatment effects the fourth year after fertilization were confounded by a dramatic reduction in budworm

Table 5. Effect of NPK fertilizer on budworm shoot severances 2, 4, and 6 years after fertilization on four study areas.

Damage	Years since fertilization	Control	NPK
		(percent)	
Shoots severed	2	25	41
	4	8	8
	6	29	32
None	2	29	22
	4	83	84
	6	37	31

populations throughout much of western Montana in 1969, the third season after fertilization. An unseasonal cold-wet spell in June of that year reduced budworm populations about 90 percent and budworm injuries up to 70 percent the following season (Fellin and Schmidt 1973b). However, western spruce budworm populations resurged rapidly following their decimation by the frost--the number of shoots severed in the control plots in year 6 were back to, and had actually exceeded, what they were in year 2 (Table 5).

The data hint that there were small residual effects of fertilization on budworm feeding in year 6--the percent of lateral severances was slightly greater on the NPK treatment and also fewer totally undamaged trees than on the control.

Terminal Shoot Damage

Budworm feeding on terminal shoots was essentially the same as that on the lateral shoots and fascicles--damage was highest on the fertilizer treatments that included nitrogen, intermediate on the PK treatment, and lowest on the control plots (Table 6). Larvae severed about one and a half to twice as many of the terminal shoots on the fertilized plots as on the controls.

Table 6. Percent of terminal shoots severed by larvae 2 years after fertilization.

Treatment	Area: Lower Cottonwood	Area: Rice Ridge
	(percent)	
NP	53	87
N	60	67
NK	53	67
Control	33	47
PK	40	73
NPK	60	67

We consider the severence of terminal shoots the most severe damage that budworm inflicts on western larch because it reduces both the rapid height growth and excellent bole form of western larch--two very desirable attributes of larch (Schmidt and Fellin 1973)(Fig. 4).

The incidence of damage was higher on the terminal shoots than on any other portions of the tree, a relationship that supports results of some of our earlier studies (Fellin and Schmidt 1973a; Schmidt and Fellin 1973). For example, at Rice Ridge, where budworm populations were high 2 years after fertilization, over three-fourths of the terminal shoots were severed on the fertilized plots compared to only about half of the lateral shoots.

Budworm Feeding Relationships

Certainly, fertilization did not deter any larval feeding on larch. Rather, all types of feeding were enhanced by fertilization, but the increases of the fertilized plots over that of the controls were least in needle feeding and greatest in the more severe form of feeding--the shoot mining and severances (Table 7). Using Lower Cottonwood as the example and a ratio of NPK/Control, the apparent increase in needle feeding due to NPK had a ratio of only about 1.14, 2 years after fertilization. At the same time, the ratio for lateral shoot mining was 1.78 and that for lateral shoot severance was 1.71.

Table 7. Effect of NPK fertilizer on type of budworm feeding, 2, 4, and 6 years after fertilization at Lower Cottonwood.

	Control			NPK		
Damage	Year 2	4	6	2	4	6
			(percent)			
None	21	84	28	10	84	24
Needle feeding	79	16	72	90	16	76
Lateral shoots mined	37	5	38	66	7	45
Lateral shoots severed	34	4	35	58	5	41

Consistent with earlier studies (Schmidt and Fellin 1973), about 90 percent of those shoots mined were also severed--the budworm nearly always succeeded in severing the shoots.

Larval feeding damaged fascicles early in the season and was directly related to the number of lateral shoots severed later in the season (Fig. 5). There was a strong linear relationship of fascicle feeding to lateral shoot severances when data from all areas and years on both the NPK and control plots were combined. For example, if about 20 percent of the fascicles were fed on, about 50 percent of the lateral shoots could be expected to be severed a little later. There was no detectable difference in this relationship between the fertilized and control plots.

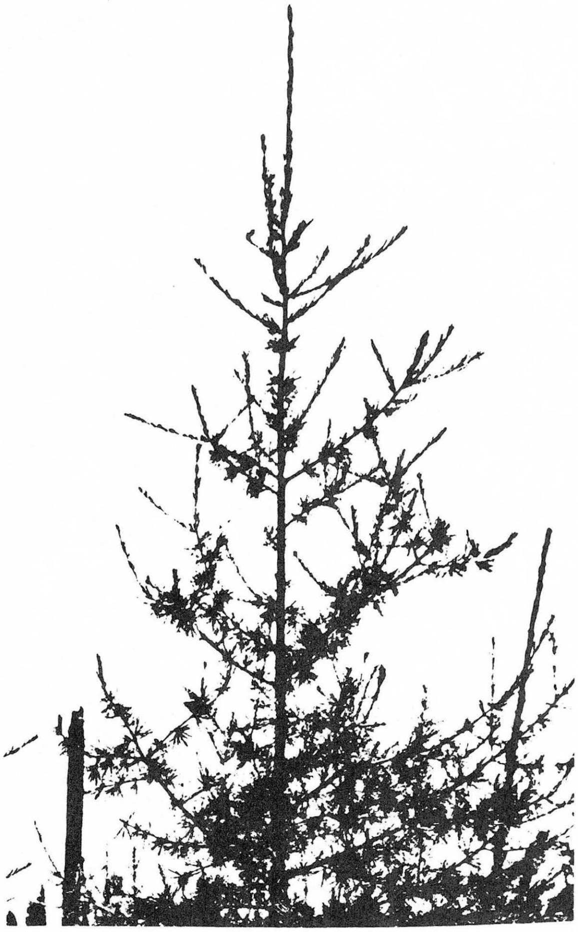

Figure 4a. Effects of western spruce budworm feeding on the form of the upper bole of western larch--no budworm feeding.

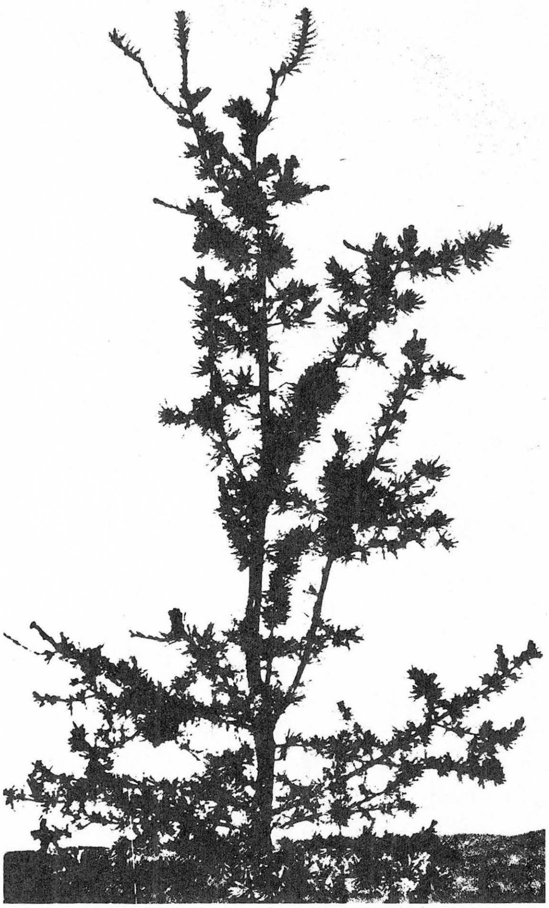

Figure 4b. Effects of western spruce budworm feeding on the form of the upper bole of western larch--repeated budworm feeding.

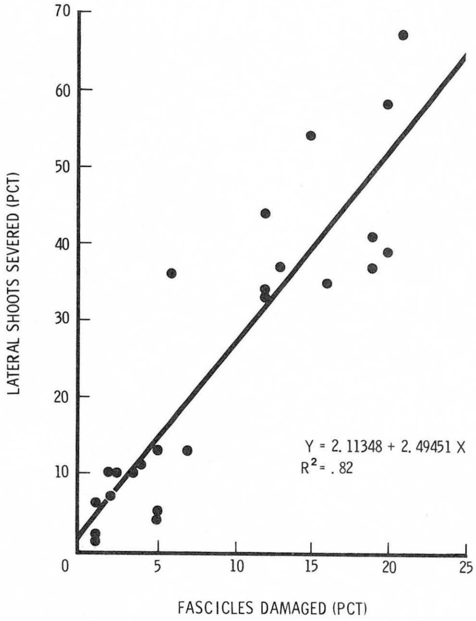

Figure 5. Relationship of the percent of fascicles fed on and the percent of lateral shoots severed by western spruce budworm larvae.

Conclusions

Fertilization is still in its infancy in forests of the Northern Rockies, but as management intensifies, it may become a practical forest management tool. Like many management practices, the introduction of fertilizers into a natural ecosystem can be expected to affect elements of the system other than that to which the practice is directed. In this study, the objective of the fertilization treatment was to accelerate tree growth, but we discovered that the fertilizers also influenced the feeding behavior of western spruce budworm larvae. Our evaluation for the first 6 years after fertilization showed that:

1. Fertilization increased all types of budworm feeding on young western larch, including fascicle feeding, needle feeding on the lateral shoots, lateral shoot mining, and severances of lateral and terminal shoots.

2. All fertilizer combinations tested resulted in increases in budworm feeding.

3. Those combinations of fertilizers that included nitrogen increased the incidence of budworm feeding the most with an intermediate effect shown by the fertilizer that had no nitrogen (PK).

4. Fertilizers that included nitrogen increased the incidence of budworm feeding in the general range of one and a half to twice that found on the control plots.

5. Fertilizer effects on budworm-feeding appeared relatively short-lived, with the effects most pronounced the second year after treatment and declining rapidly after that.

6. Practically none of the trees, even on the control plots, escaped some type of budworm feeding the second year after fertilization, a year that coincided with a generally heavy budworm infestation.

7. Budworm feeding was most pronounced in the upper crowns of both fertilized and nonfertilized trees with no apparent changes in this feeding pattern due to fertilization.

8. The effects of fertilization on budworm feeding, in relation to the controls, were relatively consistent from area to area, in spite of differences in budworm populations on the different areas.

9. The most severe forms of budworm feeding--shoot severances--were increased the most by fertilization.

10. Damage to the terminal shoots was the most pronounced of any of the damage categories, and from determinations we made from earlier studies, can be expected to have the most pronounced effect on tree development.

Why these fertilizer treatments affected the feeding behavior of western spruce budworm larvae is not explained by this study. Our study areas were relatively small and our sampling indicated that larvae were evenly distributed. Therefore, the condition of the tree--the feeding substrate for the budworm--must be the major factor affecting the budworm larvae response to the fertilizers. We postulate that at least two factors may help explain this feeding response: (1) The nutritional status of needle and shoot components of fertilized larch trees are improved by fertilization. This more favorable diet may result in more vigorous and active budworm larvae capable of increased feeding activity. (2) Budworm larvae find the fertilized trees a more favorable substrate and fewer of them disperse from the tree to the forest floor where they succumb to unfavorable physical and biological conditions.

Nutritional studies may help explain why some of these interactions between budworm larvae and fertilized trees occur. In the meantime, it appears that fertilization of larch stands within areas of heavy budworm infestation should be delayed until budworm populations decline. During a heavy infestation, the positive effects of fertilization on larch tree growth and vigor can be largely negated by increased budworm feeding.

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SPRUCE BUDWORM FECUNDITY AND FOLIAR CHEMISTRY: INFLUENCE OF SITE

M.D.C. Schmitt[1]

M.M. Czapowskyj[2]

D.C. Allen[3]

E.H. White[4]

M.E. Montgomery[5]

[1]Research Assistant, School of Forestry, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210.

[2]Principal Soil Scientist, USDA Forest Service, Northeastern Forest Experiment Station, Orono, ME 04473

[3]Professor, Department of Environmental and Forest Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210.

[4]Professor, School of Forestry, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210.

[5]Research Entomologist, USDA Forest Service, Northeastern Forest Experiment Station, Hamden, CT 06514

ABSTRACT

Two Maine spruce-fir stands having different soils were sampled to determine the relationship between spruce budworm weight (fecundity) and foliage quality. Although much of the variation in budworm weight was attributable to other factors, significant correlations between budworm weight and multiple foliar nutrient concentration variables suggest that foliage quality altering silvicultural practices such as fertilization may stimulate populations of the spruce budworm.

Introduction

One of the many questions that needs to be answered concerning the relationship between the spruce budworm (Choristoneura fumiferana Clem.) and the spruce-fir forest concerns the hypothesis that site productivity influences the susceptibility of these valuable forests to spruce budworm outbreaks. Quantification of this theoretical relationship is a highly desirable goal because the information could be used to develop a hazard rating scheme based on differential site productivity. This would facilitate decision making by forest managers or pest management specialists who must determine how and where to allocate limited time and financial resources.

In addition to the obvious variation in productivity associated with sites that have vastly different gross characteristics, it is also important to consider the more subtle variation in site productivity that may be expressed in differential foliar nutrient concentrations (Czapowskyj, 1979; Tilton, 1978). The latter is intuitively appealing because evidence suggests that nutritional, structural, and allelochemical quality of foliage consumed by budworm (Mattson and Koller, in press) may significantly alter important behavioral and population characteristics such as propensity to feed (Albert et al., 1982), survival of larvae, fecundity (Shaw et al., 1978), and oviposition (Stadler, 1974).

Forest fertilization is a means by which wood and fiber production can be increased in the spruce-fir forest. Fertilization, however, significantly alters foliar nutrient concentrations (Czapowskyj et al., 1980; Briggs et al., 1981). Inclusion of foliar nutrient information in an equation that defines the relationship between site productivity and the intensity and duration of budworm infestation would allow researchers to evaluate forest fertilization not only in the context of its primary goal of increased production, but also its impact on the spruce budworm. For example, Xydias and Leaf (1964) indicated that fertilization increased damage to white pine (Pinus strobus L.) by the white pine weevil (Pissodes strobi Peck), negating beneficial effect of this management option on tree growth and bole quality. A number of other studies have demonstrated the impact of forest fertilization and tree nutrition on insect and disease organisms (e.g., Baule, 1973; Campbell, 1976; Carrow and Graham, 1968; Cooke et al., 1978; Mitchell and Paul, 1974; Moore and Layman, 1978; Mustanoja and Leaf, 1965; Roberts and Chow, 1977; Smirnoff and Bernier, 1973; Weiner and Mirkes, 1972; White and Leaf, 1957).

The objective of our study in Maine was to quantify the relationship between selected physical characteristics of the spruce budworm and site productivity in mixed stands of red and white spruce (Picea rubens Sars.; Picea glauca (Moench) Voss.) and balsam fir (Abies balsamea (L.) Mill.) growing on two sites that differed in soil type and drainage. It is anticipated that the results of this and similar studies will contribute toward (1) the development of diagnostic criteria to evaluate the susceptibility of forest stands to budworm outbreaks based on analyses of host or site conditions and (2) elucidation of the consequences of inadvertently stimulating an increase in spruce budworm populations when spruce-fir stands are commercially fertilized.

Methods

Site Descriptions

Two study areas were selected during the 1980 field season as suitable for this investigation. The first, designated as the dry site, is located in Little Squaw Township, Piscataquis County, Maine, and is occupied by a 50-70 year-old stand consisting primarily of balsam fir and red spruce with lesser quantities of American beech (Fagus grandifolia Ehrh.) and yellow birch (Betula *alleghaniensis* Britton). Stand basal area is approximately 230 square feet/acre at a density of about 470 trees/acre, with an associated site index of 53 for red spruce and 58 for balsam fir. Understory vegetation is limited to seedlings of the overstory species in addition to a number of herbaceous species. The soils belong to the Chesuncook catena and consist of a complex of the Telos and Chesuncook series. These soils were developed in glacial till derived from slates, phyllites, and a mixture of other dark and low grade metamorphic rocks. The Telos soil is a deep, somewhat poorly drained soil with a seasonal high water table depth of about eight inches. Internal drainage is moderate through the solum of this soil, with much of the water moving laterally across the surface of very compact glacial basal till that occurs at a depth of about 16 inches, which marks the depth of maximum root penetration. The deeper Chesuncook soil has a seasonal high water table depth of about 16 inches and exhibits tree root penetration to a depth of 18 inches. A compact layer of basal glacial till occurs at a 20 inch depth. Both the Telos and Chesuncook soils are classified as coarse-loamy, mixed, frigid, Aquic Dystrochrepts.

The second area, designated as the wet site, is located in Thorndike Township, Somerset County, Maine, and is occupied by a stand of similar age and composition to that on the dry site except for the presence of sugar maple (*Acer saccharum* Marsh.) and northern white cedar (*Thuja occidentalis* L.). Stand basal area is approximately 205 square feet/acre at a density of 55 trees/acre, with an associated site index of 48 for red spruce and 49 for balsam fir. The soils also belong to the Chesuncook catena but are members of the Monarda series of coarse-loamy, mixed, frigid, Aeric Haplaquepts. On this soil, root growth is restricted to an organic mat and an underlying cobble and gravel zone 2-6 inches thick. Although the seasonal water table depth varies with local precipitation, the root zone in this soil may not drain until several days after precipitation events (Schiltz and Grisi, 1980).

Budworm/Foliage Sampling and Analysis

A total of 38 randomly selected dominant and codominant balsam fir and red spruce trees with relatively full crowns and no evidence of excessive budworm feedings or other damage were chosen for analysis. Late stage larvae (sixth instar) and pupae were collected during the period of June 30-July 15, 1980, from 45 cm long midcrown branch tips taken from the midcrown of each of the sample trees using a pole pruner with basket attachment. When the population density permitted, enough healthy insects were collected to insure that 20 female moths would be obtained from each sample tree. The pupae were weighed the day of collection or within 24 hours of formation and placed in separate cups until moth emergence, at which time moths were weighed within eight hours of ecolsion, frozen, oven-dried at 60^{0}C to constant weight, and reweighed.

Current (1980), one year (1979), and two year-old (1978) foliage for element analysis was collected in late August and early September from the upper third of the crown, Foliage analyzed for organic materials was obtained in early July from the same midcrown branches used for samples of late stage larvae. All foliage was put on ice in the field, and transferred to freezers the day of collection. Foliage for element analyses was oven-dried at 60^{0}C to constant weight and ground in a Wiley Mill equipped with stainless steel fittings to a size that permitted passage through a 1 mm sieve. Subsample foliar N concentration were determined using the macro-Kjeldahl method (Wilde *et al.*, 1972). Additional foliar subsamples were dry-ashed (Parrow, 1976) and analyzed for P using the amonium-molybdate-vanadate method (Jackson, 1958) and K, Ca, and Mg using atomic absorption spectrophotometry.

For organic analyses, freeze-dried foliage was ground to pass through a 100 micron sieve. A 70 mg subsample was mixed with 3 ml of methanol:chloroform:water (12:5:3), placed in an ultrasonic bath for ten minutes, centrifuged, and the supernatant decanted. This extraction process was repeated twice. To the combined supernatant, 2 ml chloroform and 4 ml water were added followed by mixing and centrifugation. Top layer volume was recorded and aliquots taken for phenolic and sugar analyses.

Total phenols were determined with Folin-Denis reagent using procedures recommended by Rosenblatt and Peluso (1944) on a semi-micro scale. Specifically, a 25 to 100 microliter extract was diluted with water to 7 ml followed by the addition of 0.3 ml of Folin-Denis reagent and 0.6 ml of a saturated solution of sodium carbonate. The solution was read at 730 nm after [illegible]0 min- utes against a reagent blank. Gallotannin was used as a reference standard.

Flavanol content, including dihydrochalcones and proanthocyanidin oligimers, was determined with freshly prepared 1% vanillin in 70% sulfuric acid reagent (Swain and Hillis, 1959). A 25 microliter extract was added to each of two test tubes containing 1 ml water in an ice bath. One tube received 2 ml of reagent and the other 2 ml 70% sulfuric acid followed by mixing. The tubes were removed and read after 15 minutes against a blank of 25 microliters methanol, 2 ml reagent, and 1 ml water. Catechin served as a reference standard.

Condensed tannin content was estimated by forming anthocyanidins. This was accomplished by heating a 50 to 200 ml sample of extract in 5 ml of 5% concentrated hydrochloric acid in 1-butanol for 1.5 hrs at 95^{0}C. The sample was read at 548 nm against a reagent blank. Correction for interfering pigments prevalent in early season samples was made by placing the sample in acetic acid, ethanol, 1-butanol, (1:3:16). A purified condensed tannin from July red oak leaves served as a reference standard.

Sugars were analyzed by gas chromatography. A 4 ml aliquot of extract was dried under nitrogen and silylated sugar oximes formed using hydroxylamine hydrochloride and hexamethyldisilazane in pyridine (Pierce Handbook and General Catalog, 1979-80). Phenyl-Beta-glucopyranoside was added as an internal standard and commercially available reagent grade sugars serves as references. Chromatography was on a 2 m x 2 mm column of 3% OV-17 using a temperature program of 170 to 275^{0}C at 10 C/min with detection by FID. Peak areas were integrated to mg/sample by the internal standard method.

Statistical Analyses

Using foliar nutrient concentration as measures of site productivity, Pearson correlations (Snedecor and Cochran, 1967) were generated to relate average pupal wet weight, moth wet weight, and moth dry weight to the N, P, K, Ca, Mg, fructose, glucose, sucrose, total free sugar, total phenol, flavanoid, and condensed tannin concentrations in the foliage from the different age classes on an individual tree basis aross both sites and species. Additionally, general linear models were constructed to determine which factors accounted for a significant amount of the variation in the budworm variables. In addition to the foliar nutrient concentration values, dummy variables that defined the different study sites and species examined were tested for inclusion in these models (Freund and Littell, 1981).

Results and Discussion

The correlation coefficients between the budworm and foliar nutrient concentration variables are provided in Table 1. Both budworm variables were highly significantly correlated with foliar N concentrations in all foliage age classes. The strongest correlations occurred in current year foliage. Both budworm variables were also highly significantly correlated with glucose, fructose, and total free sugar concentrations in current year foliage. These findings are consistent with the results of Harvey (1974, 1975), Shaw and Little (1977), and others, who demonstrated that the spruce budworm develops better on foliage that contain sugars and nitrogenous compounds at higher levels. Both budworm variables were also significantly correlated with Mg, total phenol, and flavanoid concentrations in current year foliage, while pupal weight was significantly correlated with P, Ca, and condensed tannin levels in current year foliage and with K concentrations in two year-old foliage. In all cases the significant correlation coefficients were positive. While it was not surprising to find pupal weights positively correlated with nutrients and carbohydrates since these are required for growth, the positive correlation with phenolic and tannin levels was unexpected. These compounds supposedly function as digestion inhibitors by binding with protein (Feeney, 1969); hence, would be expected to be negatively correlated with weight gain.

The data indicate that foliage with higher nutrient concentrations is likely to foster development of spruce budworm pupae and moths with greater individual mass and, presumably, fecundity. This suggests that high foliar nutrient concentrations caused by inherent differences in site quality or the result of silvicultural practices such as fertilization may increase the fecundity of the spruce budworm to such an extent that the net effect of such practices may actually be a reduction in wood and fiber production.

The linear models containing the factors that account for a significant amount of the variation in the budworm variables are provided in Table 2. The model with pupal weight as the dependent variable produced an r-square value of 0.29, while the model with moth dry weight as dependent variables yielded a r-square of 0.69. In both models, the dummy variables specifying site and specific differences were statistically significant. The only

Table 1. Pearson correlation coefficients between pupal weight or adult dry weight and foliar chemistry.

	Pupal wet weight Foliage age			Pupal dry weight Foliage age		
	Two-year	One-year	Current	Two-year	One-year	Current
N	0.471***	0.520***	0.634***	0.460***	0.849***	0.583***
P	-0.094	-0.025	0.415	-0.248	-0.205	0.197
K	0.355**	0.191	-0.365	0.254	0.176	-0.144
Ca	-0.063	0.046	0.466***	-0.163	-0.050	0.308
Mg	-0.036	0.217	0.567***	-0.029	0.201	0.493***
Fructose	0.487	-----	0.688***	0.422	-----	0.621**
Glucose	-0.109	-----	0.750***	0.649**		
Sucrose	0.139	-----	0.347	0.124	-----	0.263
Total free sugars	0.319	-----	0.731***	0.272	-----	0.706***
Total phenols	0.105	-----	0.634**	0.207	-----	0.483*
Flavanoids	-0.281	-----	0.614**	-0.183	-----	0.501*
Condensed tannins	0.438	-----	0.502*	0.551	-----	0.440

*, **, and *** indicate significance at the alpha = .10, .05, and .01 levels, respectively.

foliar nutrient concentration value that contributed a significant amount of information about the budworm variables after differences due to site and species were accounted for was the K level in current year foliage, which was included in the model where moth dry weight was the dependent variable. The significant relationship between budworm variables and concentrations of foliar chemicals (Table 1) are totally masked by the inclusion of dummy variables specifying site and species differences. However, these variables have likely achieved significance due to the significant differences in nutrient concentrations that exist between sites (Table 3) and species (Table 4).

Table 2. Significant sources of variation in pupal weight and moth dry weight including estimates of regression coefficients and means.

Dependent Variable: Pupal Weight (g) r^2=0.29

Parameter	Estimate	Std. Error	T value	P > T
Intercept	0.0499	0.0035	14.39	0.0001
Site	0.0105*	0.0041	2.56	0.0159
Species	0.0101#	0.0040	2.53	0.0172

Table 2. continued

Dependent Variable: Moth Dry Weight (g) r^2=0.69

Parameter	Estimate	Std. Error	T value	P > T
Intercept	0.0018	0.0039	0.45	0.6556
Site	0.0040*	0.0014	2.89	0.0106
Species	0.0084#	0.0018	4.71	0.0002
K levels in current year foliage	0.0111	0.0043	2.61	0.0190

	Pupal Weight		Adult Dry Weight	
Site	Mean	Std. Error	Mean	Std. Error
Dry	0.066	0.003	0.018	0.001
Wet	0.056	0.003	0.013	0.001
Species				
Balsam Fir	0.064	0.003	0.020	0.001
Red Spruce	0.054	0.003	0.013	0.001

---

*Multiply by 1 if site = dry, 0 if site = wet.
#Multiply by 1 if species = balsam fir, 0 if species = red spruce.

Table 3. Mean concentrations (%) of foliar chemicals in current, one and two year-old foliage by site.

	Two year		One year		Current	
	Dry	Wet	Dry	Wet	Dry	Wet
N	1.133	1.022*	1.221	1.110*	1.260	1.156
P	0.082	0.105*	0.092	0.111*	0.120	0.139
K	0.486	0.504	0.556	0.597	0.737	0.910
Ca	0.612	1.280*	0.760	1.405*	0.572	0.605*
Mg	0.103	0.142*	0.149	0.188*	0.175	0.155
Fructose	1.704	1.349	1.383	1.928	1.866	1.256
Glucose	3.016	3.270	2.450	1.652	3.591	0.999*
Sucrose	0.627	0.674	0.058	0.118	0.401	0.056
Total free sugars	5.345	5.171	4.890	3.700	6.005	2.311*
Total phenols	8.050	8.375	6.290	4.300	4.228	3.068*
Flavanoids	6.950	8.668	5.550	3.050	3.905	2.263*
Condensed tannins	5.800	5.148	3.540	3.100	2.902	2.282

---

*Indicates statistical significance between site at the alpha = 0.05 level.

Table 4. Mean concentrations (%) of foliar chemicals in current, one and two year-old foliage by species.

	Two year		One year		Current	
	Fir	Spruce	Fir	Spruce	Fir	Spruce
N	1.261	0.870*	1.304	0.990*	1.420	1.119*
P	0.097	0.098	0.101	0.108	0.136	0.129
K	0.533	0.463	0.578	0.589	0.637	0.906*
Ca	1.467	0.611	1.775	0.605*	1.032	0.418*
Mg	0.147	0.111	0.226	0.125*	0.245	0.132*
Fructose	1.420	-----	1.383	1.928	2.030	1.479*
Glucose	3.219	-----	2.450	1.652	5.555	1.313*
Sucrose	0.665	-----	0.058	0.118	0.720	0.069*
Total free sugars	5.206	-----	4.890	3.700	8.307	3.001*
Total phenols	8.310	-----	6.290	4.300	6.014*	2.755*
Flavanoids	8.324	-----	5.550	3.050	5.320*	2.377*
Condensed tannins	5.278	-----	3.540	3.100	3.646*	2.219*

---

*Indicates statistical significance between species at the alpha = 0.05 level.

Examination of respective site and species means indicated that pupae and moths from the dry site were significantly heavier than those from the wet site, and pupae and moths from balsam fir trees were significantly heavier than those that fed on red spruce. Although both site and species factors are significant, the differences attributable to species are greater than those due to site.

Conclusions

The results of this study support the hypothesis that size (fecundity) of the spruce budworm adults is, in part, related to site productivity as measured by obvious physical differenes in sites and/or foliar nutrient concentrations. The budworm variables examined in this study were significantly correlated with a number of foliar nutrient concentration values. Dummy variables that specified differences in sites and species sampled were statistically significant for all budworm variables examined in general linear models designed to identify sources of variation in budworm characteristics.

However, r-square values for the linear models are not satisfying, in that a large proportion of the variation in the budworm variables could not be accounted for by differences in site productivity as expressed by the variables selected. This, however, is not unexpected in view of the diverse extrinsic and intrinsic factors that may influence budworm fecundity (Miller, 1963). Furthermore, similar relationships must be determined for a range of site conditions and budworm population histories to assure that the results obtained are representative of and applicable to a broader range of field conditions. This is especially important in view of interstand differences that may exist in regression models that describe fecundity as a function of budworm size (Miller, 1957). Numerous studies have demonstrated a relationship between insect fecundity and food quality. The question that must be addressed now concerns the biological significance of statistically significant results. For example, how many eggs are represented by a difference of 0.010 g in mean pupal weight? Is this difference enough to significantly alter the population dynamics of the budworm?

Although experimental results are not conclusive and are based on a limited number of samples, evidence suggests that those interested in improving spruce-fir forest productivity through fertilization will need to balance the opportunity to generate additional revenue from increased outputs of wood and fiber against the possibility that elevated foliar nutrient concentrations will stimulate destructive populations of the spruce budworm.

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THE INFLUENCE OF HERBIVORY ON THE NET RATE OF INCREASE OF GYPSY MOTH ABUNDANCE: A MODELING ANALYSIS

Harry T. Valentine

Research Forester, Northeastern Forest Experiment Station, Center for Biological Control of Northeastern Forest Insects and Diseases, 51 Mill Pond Road, Hamden, CT 06514

A differential equation model of gypsy moth abundance, average larval dry weight, and food abundance was used to analyze the effects of changes in foliar chemistry on the net per capita rate of increase in a gypsy moth population. If relative consumption rate per larva is unaffected by herbivory, a reduction in the nutritional value of foliage reduces the net rate of increase at relatively low larval densities, and increases the larval density needed to bring about starvation. This result is achieved by reducing larval assimilation efficiency, or by increasing larval death rate, or both, in response to declining nutritional value of foliage associated with herbivory. An increase in relative consumption rate in response to herbivory reduces the larval density needed to bring about starvation, and reduces the net rate of increase of the larval population at all higher larval densities.

Introduction

Oak (Quercus spp.) foliage is the principal food of the gypsy moth (Lymantria dispar (L.)) in Eastern North America. Herbivory causes changes in the concentrations of suspected primary and secondary metabolites of gypsy moth in the foliage of oaks (Schultz and Baldwin, 1982; Valentine et al., 1983). Late-instar gypsy moths that feed on severely defoliated oaks are smaller at pupation, and less fecund, than gypsy moths that feed on essentially undefoliated trees (Wallner and Walton, 1979). Together, these results suggest that changes in foliar chemistry induced by herbivory influence the population dynamics of gypsy moth during outbreaks and the subsidences of outbreaks. The exact nature of the influence is neither known nor obvious because it is intermingled with the influences of parasites, predators, disease, and food shortage. However, it should be possible to discern some of the effects of induced changes in foliar chemistry on gypsy moth population dynamics through modeling.

The Model

The basic model that I use consists of a system of differential equations. The equations describe changes in larval dry weight, larval abundance, and available foliage with respect to time measured in days (t), where 1 day is assumed to equal 15 Celsius degree days (threshold = 4.4^{o}). The equations are initialized at the start of each larval generation and solved over the interval $0 \leq t \leq 44$. It is assumed that all larvae hatch and start feeding coincident with budbreak at t=0, and that all surviving larvae pupate at t=44. The values of the components at t=44 are used to predict the initial values of the components for the next generation. For example, the initial number of larvae next year is predicted from the number of pupae this year.

The variables of the model are:

$W(t)$ = average dry weight of a larva (mg)
$F(t)$ = expected dry weight of a leaf (mg)
$F^*(t)$= total amount of foliage available (mg)
$X(t)$ = number of gypsy moth larvae feeding on $F^*(t)$

$C_{max}(t)$ and $C_{act}(t)$ are maximum and actual consumption rates (mg/day) of the larval population, which are defined in terms of the variables of the model.

The variables are related as follows:

$$C_{max} = a_1WX \qquad (1)$$

$$C_{act} = \min(C_{max}, a_2F^*) \qquad (2)$$

$$dX/dt = -X(a_3+a_4(1-C_{act}/C_{max})) \qquad (3)$$

$$dW/dt = E(C_{act}/X)-a_5W \qquad (4)$$

$$dF/dt = a_6F(\ln F)(1-(\ln F)/a_7) \qquad (5)$$

$$dF^*/dt = (F^*/F)dF/dt-C_{act} \qquad (6)$$

In the absence of a shortage of food, the consumption rate of a larva is a_1W (Valentine and Talerico, 1980), and the consumption rate of the larval population (C_{max}) is a_1WX (eq. 1). If the consumptive demand of the larval population approaches or exceeds available foliage (i.e., $C_{max} > a_2F^*$), herbivory is constrained at rate a_2F^* (eq. 2), and the consumption rate of a larva is a_2F^*/X.

Since gypsy moth is univoltine, and dispersal is assumed nil, all changes in the abundance of feeding larvae are negative. By equation (3), larvae die at rate a_3X from the effects of density-dependent agents, and, during a food shortage, larvae cease to feed (and starve) at rate $a_4(1-C_{act}/C_{max})X$.

Average larval growth (eq. 4) is equal to the average larval anabolic rate minus the average larval catabolic rate (a_5W). The anabolic rate is the product of the larval consumption rate (C_{act}/X) and assimilation efficiency (E). Foliage quality should influence larval growth through its effect on E; various predictors of E are described in the next section.

Equation (5) describes the growth of an average-size leaf (Valentine, 1983), and equation (6) describes the collective growth of (say) N leaves available to the larval population. In the absence of larval feeding, the relative rates of increase in dry weight in the average leaf and the N leaves are equal (i.e., $dF^*/F^*/dt = dF/F/dt$), and the solutions of (5) and (6) are related as $F^*(t)=NF(t)$. When the gypsy moth feeds, the growth of available foliage is reduced by the rate of consumption (C_{act}), and $F^*(t) < NF(t)$ for $t > 0$. Rationale for the formulation of (6) was reported by Goldstein and Van Hook (1972), Nagy (1978), and Valentine (1978). Apparent herbivory (H) can be calculated from the solutions of (5) and (6) as:

$$H = (1-(F^*(t)/N)/F(t)) \tag{7}$$

The solution of equation (5) can be written as

$$\ln F(t) = a_7/(1+\exp(a_8-a_6t)) \quad 0 \leq t \tag{8}$$

Therefore, (5) can be eliminated from the model by substituting for $(dF/dt)/F$ on the right hand side of (6) with:

$$(dF/dt)/F =$$

$$a_6a_7(\exp(a_8-a_6t)/(1+\exp(a_8-a_6t))^2 \tag{9}$$

At budbreak (t=0), average leaf dry weight is

$$F(0) = \exp(a_7/(1+\exp(a_8))) \tag{10}$$

To initialize $F^*(t)$, it is convenient to put the variables of the model on a per-ha basis. If we denote the asymptotic dry weight of mature foliage per ha as F^*_{max}, then total available foliage at budbreak is:

$$F^*(0) = F(0)F^*_{max}/\exp(a_7) \tag{11}$$

To solve the model over a period of years, a function is needed that predicts initial larval abundance (X(0)) in year n+1 from pupal abundance (X(44)) in year n, viz.:

$$X(0)_{n+1} = a_9W(44)_nX(44)_n \tag{12}$$

The parameter a_9 subsumes survival rates of pupae, adults, and eggs, and the proportion of females in the adult population; egg production is a linear function of pupal weight (Hough and Pimentel, 1978).

Solutions of the Model

One way to discern the effects of food quality on gypsy moth population dynamics is to compare solutions of the model with and without the effects of food quality included, while holding other effects constant. Unless noted otherwise, the following solutions were computed with the parameter values listed in table 1, and with W(0) = 0.2 mg, and $F^*_{max} = 10^9$ mg/ha.

Assuming that food quality is invariant between years and unaffected by herbivory, a purely empirical expression describing assimilation efficiency of larvae for eq. (4) is the cubic polynomial (adapted from Valentine and Talerico, 1980):

$$E = a_{10}+a_{11}t+a_{12}t^2+a_{13}t^3 \tag{13}$$

The model of gypsy moth abundance without food quality effects is now completely defined.

Inspection of the model shows that where food is unlimited, the net per capita rate of increase (1/yr) in the abundance of feeding larvae (X) from t=0 in year n to t=0 in year n+1 is constant:

$$\ln(X(0)_{n+1}/X(0)_n) =$$

$$-a_3 44+\ln(a_9)+\ln(W(44)_n) \tag{14}$$

When the initial larval density in year n is sufficient to cause a food shortage, the right hand side of (14) no longer applies, as the net per capita rate of increase declines precipitously (Fig. 1). Over a period of years, X(0) assumes a pattern such as depicted in Figure 2; i.e., X(0) increases exponentially from year to year until food becomes limiting to late-instar growth and survival, causing a catastrophic decline in X(0) the following year, and a resumption of exponential population increase. However, it is evident in Figure 1 that the net per capita rate of increase can be zero, so a steady state population is theoretically possible.

As was noted, herbivory causes changes in foliar chemistry which reduce larval growth and pupal weight. We can produce such an effect by forcing larval assimilation efficiency to decrease as herbivory increases. The only change we need to make is to substitute E' for E in (4) where

$$E' = E(1-a_{14}H) \qquad 0 < a_{14} \ll 1 \tag{15}$$

Under the assumptions and constraints of the model, it is obvious that this function will cause per capita fecundity to decline with increased herbivory, because fecundity is a

Table 1.--Values of parameters used to generate solutions of the model.

Parameter	Value	Source of value or data
a_1	1.003	Valentine and Talerico (1980)
a_2	0.5^a	Sensitivity Analysis
a_3	0.08	Campbell (1981)
a_4	4.0^a	Sensitivity Analysis
a_5	0.0192	Valentine and Talerico (1980)
a_6	0.265	Valentine (1983)
a_7	6.109	Valentine (1983)
a_8	0.893	Valentine (1983)
a_9	2.5	Campbell (1981)
a_{10}	0.2885	Valentine and Talerico (1980)
a_{11}	-1.0635×10^{-2}	Valentine and Talerico (1980)
a_{12}	2.4861×10^{-4}	Valentine and Talerico (1980)
a_{13}	-2.3609×10^{-6}	Valentine and Talerico (1980)

[a] Values of a_2 and a_4 were guessed and then adjusted to give larvae that survived starvation a reasonable dry weight.

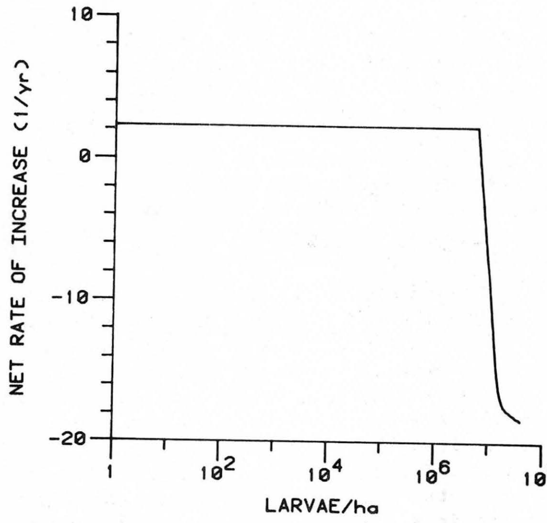

Figure 1.--Net rate of increase in larval density versus larval density as predicted by the model without foliage quality effects included.

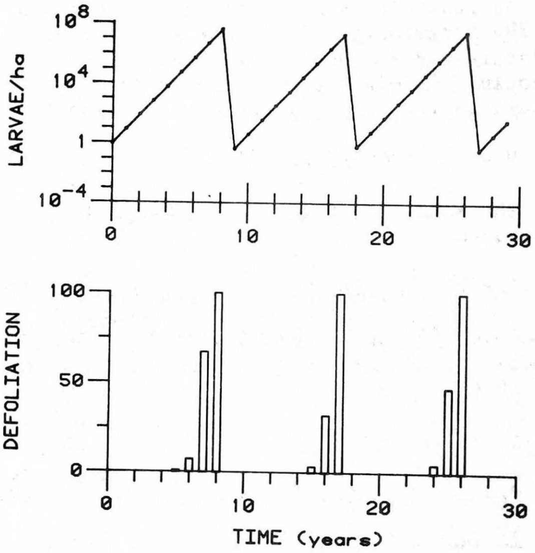

Figure 2.--Time-series of larval densities and defoliation as predicted by the model without foliage quality effects included.

linear function of pupal weight. The effect of this function on the net per capita rate of increase of the population is less obvious, but is shown in Figure 3 for a_{14} equal to 0 (no effect), 0.09, and 0.18. On the basis of experimental results reported by Wallner and Walton (1979) and by Valentine et al. (1983), I estimate the true value of a_{14} to be 0.09.

At relatively low initial larval densities, the net per capita rate of increase (for $a_{14} > 0$) is less than the corresponding rate that would be expected in the absence of a larval response (a_{14}=0) to changes in foliar chemistry induced by herbivory (Fig. 3). However, at relatively high larval densities, the net rate of increase is greater with a

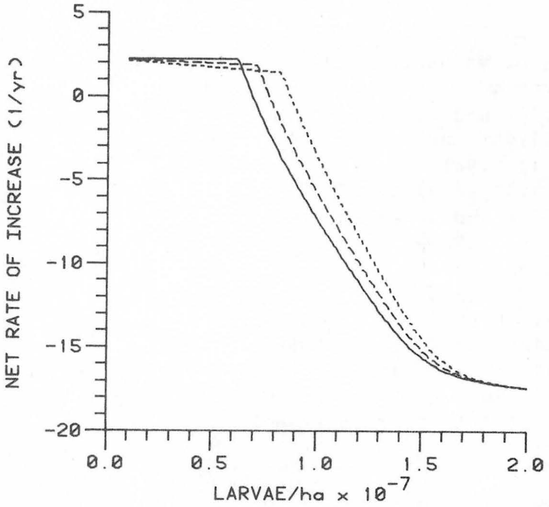

Figure 3.--Net rate of increase in larval density versus larval density when a reduction in larval assimilation efficiency associated with herbivory is included in the model (see eq. (15)). The 3 curves represent no response to herbivory (solid, a_{15}=0.0), the estimated true response to herbivory (long dash, a_{15}=0.09), and an exaggerated response to herbivory (short dash, a_{15}=0.18), respectively.

response to herbivory because fewer individuals die from starvation. Average larval consumption rate is proportional to larval weight, so starvation becomes less likely at a given population density if larvae respond to herbivory with a reduction in assimilation efficiency, but no change in relative consumption rate. The relatively inefficient assimilators weigh less than they would in the absence of the response and, therefore, are less likely to eat all the available foliage. Consequently, a reduction in larval abundance due to starvation may be postponed by a year, affording the gypsy moth additional opportunity to spread its infestation through the dispersal of first instars. The reduction in the net rate of increase in response to herbivory also tends to reduce the chance of starvation during the early instars of the next generation, and increase the chance that a larva will live to pupation. Therefore, reductions in the population through starvation may be smaller with a response to herbivory than without one. At very high initial larval densities, the model indicates that changes in foliar chemistry have virtually no effect on the net rate of increase.

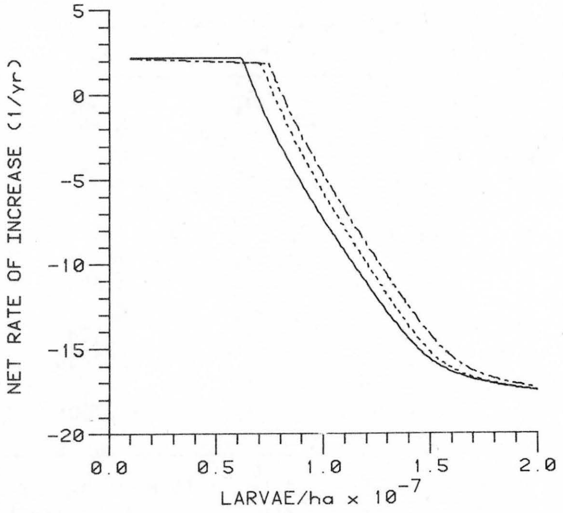

Figure 4.--Effects on herbivory on the net rate of increase in larval density. No effect (solid line); reduced assimilation efficiency with no change in relative consumption rate (short dash), and no change in assimilation efficiency, but a reduction in relative consumption rate (short dash, long dash).

The most plausible explanation for the decline in larval growth associated with herbivory is a reduction in larval assimilation efficiency. However, it is possible that assimilation efficiency is unaffected and larvae simply reduce their feeding rate in response to herbivory. The models for the two cases are similar, but not identical. Assuming no food shortage, where assimilation efficiency is affected by herbivory, we have

$$C_{max} = a_1 WX \qquad (17)$$

and

$$dW/dt = E(1-a_{14}H)a_1W-a_5W \qquad (18)$$

If feeding rate is reduced, but assimilation efficiency is unaffected, we have

$$C_{max} = a_1(1-a_{14}H)WX \qquad (19)$$

and

$$dW/dt = Ea_1(1-a_{14}H)W-a_5W \qquad (20)$$

Thus, in both cases, larval growth (dW/dt) is the same. However, the feeding rate (C_{max}) of the larval population declines with herbivory in the latter case and, therefore, larval death due to starvation is less likely at a given larval density (Fig. 4).

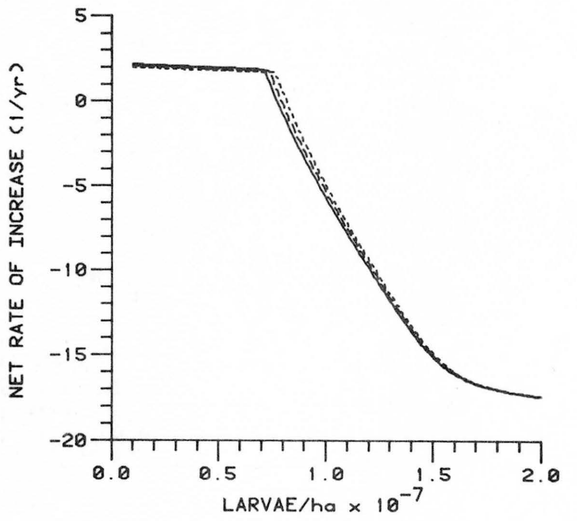

Figure 5.--Net rate of increase in larval density versus larval density when the effect of defoliation in the prior year (long dash) or 2 prior years (short dash) is added to the model (see eq. (21)). Both curves are estimated true responses. No effect due prior defoliations is represented by the solid line.

Additional reductions in pupal weight and fecundity due to consecutive defoliations (as reported by Wallner and Walton, 1979) tend to exacerbate the response of the larval population to herbivory in terms of its net per capita rate of increase (Fig. 5). The effects shown in Figure 5 were achieved by replacing a_{10} in eq. (13) with a_{10}' where

$$a_{10}' = a_{10} - a_{15}H(44)_{n-1}(1+H(44)_{n-2}) \qquad (21)$$

A parameter value of $a_{15} = .002$ gives percentage reductions to $W(44)_n$ due to defoliations in year n-1 and year n-2 consistent with the results of Wallner and Walton (1979). The implicit assumption here is that changes in foliar chemistry due to defoliation in the prior year or 2 prior years affects the assimilation efficiency of larvae in the current year. If we solve the model over a period of years, the time series of X(0) is so similar to that shown in Figure 1 that it does not warrent a figure of its own. However, the more or less constant 9-year cycle shown in Figure 1 becomes an alternating 8- or 9-year cycle when food quality effects are added.

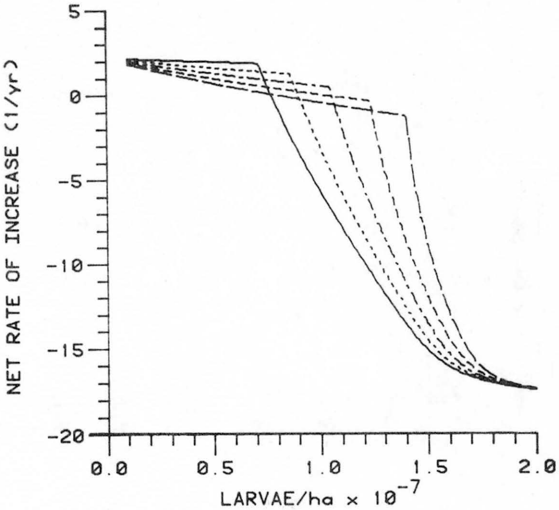

Figure 6.--The effect of an increase in larval death rate associated with herbivory (see eq. (22)) on the relation between net rate of increase in larval density and larval density for a_{16}=0.0 (solid), 0.02 (short dash), 0.04 (dot dash), 0.06 (mid-sized dash), and 0.08 (longest dash).

It has been hypothesized that changes in foliar chemistry induced by herbivory increase the rate of death of larvae from malnutrition, parasitism, and disease (e.g., Podgwaite, 1981; Schultz and Baldwin, 1982). If we assume that the per capita death rate increases with herbivory, we can assess the consequences of this larval response by replacing a_3 on the right hand side of eq. (3) by a_3' where

$$a_3' = a_3 + a_{16}H \qquad (22)$$

The effect of an increase in larval death rate associated with herbivory on the net rate of increase of the population is shown in Figure 6 for a_{16} equal to 0 (no effect), 0.02, 0.04, 0.06, and 0.08. The result is a familiar one; the net rate of increase of the population is reduced by the increase in death rate until the larval density is reached where starvation would be manifested in the absence of the increase. At higher larval densities, the net per capita rate of increase is greater because reductions in the population due to starvation are either postponed or buffered by death of larvae from other causes. Indeed, when a_{16} was assigned a value of 0.06 or 0.08, the increased death rate associated with herbivory effectively prevented the population from growing large enough to collapse from starvation (Fig. 7); instead, the population settled into a steady state. As a_{16} is increased further, the steady-state population is smaller and severe defoliation is prevented, but this is contrary to our experience with gypsy moth.

It is not known whether gypsy moth larvae respond to a reduction in the nutritional value of foliage with an increase in relative consumption rate, but Scriber and Slansky (1981) indicated that tree feeders are limited in their ability to do this. The only structural change we need to make to the model to assess the effects of increased larval consumption rate is to replace a_1 in eq.

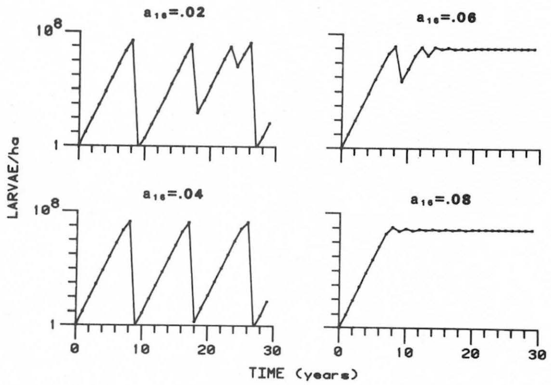

Figure 7.--Time-series of larval densities with increases in larval death rate associated with herbivory included in the model.

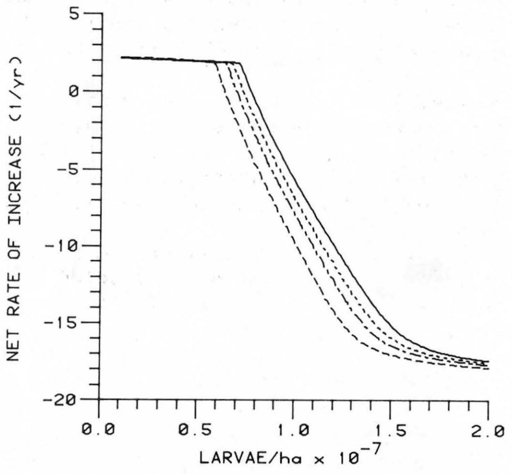

Figure 8.--Net rate of increase in larval density versus larval density where larval relative consumption rate increases with herbivory (see eq. (23)). Solutions are plotted for a_{17}=0 (solid), 0.1 (dot), 0.2 (dot-dash), and 0.4 (dash).

(1) by a_1' where

$$a_1' = a_1+a_{17}H \qquad (23)$$

Any increase in consumption rate associated with herbivory requires a compensatory reduction in assimilation efficiency so that W(44) will equal its expected value. Thus, the parameter a_{14} of eq. (15) will vary directly with a_{17}, though not linearly. The effect of this hypothesized larval response on the net per capita rate of increase of the larval population (given a_{16}=0) is shown in Figure 8 for a_{14}=0.09, a_{17}=.0; a_{14}=0.18, a_{17}=0.1; a_{14}=0.26, a_{17}=0.2; and a_{14}=0.40, a_{17}=0.4. At low larval densities, where herbivory is negligible, the effect of the larval response on the net rate of increase also is negligible. However, increases in larval consumption rate reduce the larval density needed to bring about starvation, and reduce the net rate of increase of the larval population at all higher larval densities.

Summary and Conclusions

If the parametrization of the model is adequate, the following conclusions can be drawn from this analysis. Where larval density is insufficient to cause starvation, larval response to herbivory results in a reduction in per capita fecundity, which singly, or in combination with increased larval death rate, reduces the net rate of increase in gypsy moth abundance. Unless larval relative consumption rate increases in response to herbivory, the net rate of increase in gypsy moth abundance is greater at all larval densities where larval starvation would ensue in the absence of any larval response, because a reduction in assimilation efficiency or feeding rate--or an increase in larval death rate--in response to herbivory effectively reduces the cumulative consumption of the larval population. If larval relative consumption rate does increase in response to herbivory, then, compared to no increase, the larval density needed to bring about starvation is reduced and the net rate of increase is reduced at all higher densities.

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FOLIAGE QUALITY AND ITS EFFECT ON BUDWORM POPULATIONS: A MODELLER'S VIEWPOINT

Richard A. Fleming

Environment Canada, Canadian Forestry Service, Forest Pest Management Institute, Sault Ste. Marie, Ontario, Canada P6A 5M7

Although it may soon be possible to alter stand foliage quality and thus reduce budworm reproductivity, the impact of such changes on the budworm-forest system remains unclear. There are currently a number of hypotheses concerning the key biological mechanisms which drive the budworm-forest system. The possible effects of changes in foliage quality are examined for four such alternative hypotheses. Each hypothesis suggests that in the short-term reducing foliage quality will lengthen the interval between outbreaks, increase the rate of stand wood volume production, and increase outbreak severity--and overall, improve the budworm problem in economic terms. The situation for the long-term is less certain: in some circumstances reducing foliage quality may even aggravate the budworm problem from an economic viewpoint.

Introduction

The eastern spruce budworm, *Choristoneura fumiferana* (Clem.), is a naturally outbreaking defoliator of spruce *(Picea* spp.) and balsam fir *(Abies balsamea* [L.] Mill.) in the boreal forests of eastern North America. Epidemic populations severely defoliate their host trees over wide areas causing reduced growth, top kill, and tree mortality which often results in considerable economic difficulties for the forest industry (Irland 1980).

Aerial application of insecticide has been the principal means of controlling budworm damage since the early 1950's. However, concerns about environmental impacts and cost-effectiveness (e.g., Swenson 1980) have motivated a search for possible alternative control methods. It has long been recognized that stands differ in their likelihood of budworm damage (Balch 1946; Morris 1963, pp. 189-292) and more recently it has been observed that several important nutritional parameters vary with needle age, tree species, stand maturity and other factors affecting budworm development and density (Kimmins 1971; Shaw et al. 1978; White 1974). As a consequence it has been suggested that certain stand characteristics could be manipulated through selective breeding (e.g., Zobel 1982) or fertilizer application (e.g., Shaw et al. 1978) to "favorably" alter budworm-forest dynamics. But before much investment in such research, it seems prudent to anticipate how changes in stand characteristics might affect the budworm-forest system.

This paper explores the impacts that changes in one such stand characteristic, foliage quality, might have on budworm-forest dynamics. Here foliage quality refers to the rate at which increases in foliage consumption per budworm are accompanied by increases in budworm reproductivity.

Anticipation of the effects of reducing foliage quality requires some understanding of the biological mechanisms underlying budworm-forest dynamics. Currently, there is considerable disagreement regarding the relative importance of these mechanisms. Blais (1974) concludes that budworm outbreaks require extensive areas of mature stands of balsam fir; Baskerville (1976) and Jones (1979) stress the effects of background predators; Stedinger (1977) suggests that all outbreaks are triggered by moth invasions; and Royama (1982) implies that a complex of numerically responding parasitoids and diseases may be a "universal cause" of budworm oscillations. Baskerville, Blais, Jones, and Stedinger assume that the depletion of food and ovipositing sites resulting from defoliation and tree mortality cause outbreak collapse.

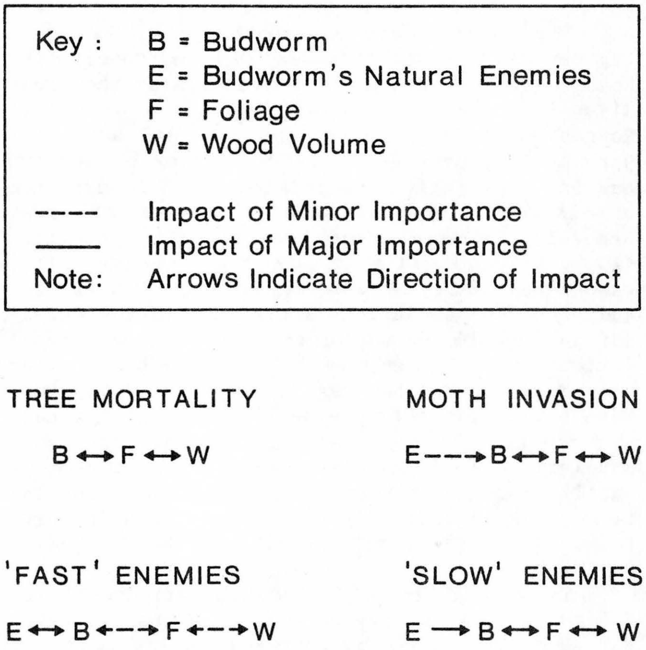

Figure 1. Hypotheses concerning the underlying mechanics of budworm-forest dynamics. The major components and their interactions are shown.

Figure 1 illustrates the assumed interactions between the principal components of the budworm-forest ecosystem for four hypothetical outbreak generating mechanisms. The 'tree mortality' hypothesis (Blais 1974) implies important and reciprocal impacts between budworm and foliage, and between foliage and wood volume. In the 'slow enemies' hypothesis, Baskerville (1976) and Jones (1979) suggested that polyphagous non-synchronized predators and parasites limit the increase of low density budworm populations. Between outbreaks, these background enemies maintain their numbers by feeding on alternate prey as well as on budworm. During outbreaks, the numbers of budworm enemies increase much more slowly than budworm numbers so 'per capita' budworm losses to predation and parasitism decrease substantially. The lack of an arrow pointing from budworm to its slow enemies in Figure 1 reflects the assumed insignificance of the slow enemy numerical response to budworm densities.

Stedinger's (1977) moth invasion hypothesis (Fig. 1) encapsulates the behavior of his large scale simulation model of budworm-forest dynamics. In contrast to Baskerville and Jones, he concluded that the impact of natural enemies on budworm-forest dynamics was less important than that of moth invasion in terms of driving the outbreak cycle. According to his model, invasion is a prerequisite for outbreak: without it, low density mortality factors extinguish small budworm populations. Sufficient budworm invasion raises local populations to densities where these mortality factors are less important; population increase then continues until outbreak levels are reached, even in the absence of further moth immigration.

The 'fast' enemies hypothesis of Figure 1 represents a simplification of the conclusions Royama (1982) reached after reanalysing the Green River Project data (Morris 1963). According to Royama, mortality due to the combined action of parasitoids, pathogens, and a complex of unknown causes "apparently associated with the occurrence of disease(s) of an unknown nature is the most probable universal cause of population oscillation". The implication is that the mortality associated with certain synchronized parasitoid and pathogen populations increases quickly enough during budworm outbreaks to return budworm populations to low densities before resource limitation necessarily becomes important. Since budworm population collapse deprives these fast natural enemies of their principal food, fast enemy populations fall soon afterwards. A pattern of oscillations in natural enemy - budworm population sizes typical of predator-prey relationships (e.g., Krebs 1972, pp. 247-254) arises.

In what follows, I study the effects of reducing foliage quality on budworm-forest dynamics for each hypothesis illustrated in Figure 1. I hope to identify the range of impacts that can be expected on both a short and a long term basis.

A Simple Budworm-Forest Model

I begin by introducing a simple idealized model of the budworm-forest ecosystem. It will provide a standard of comparison by which to consider the complexity of budworm-forest dynamics in the field. Adopting a philosophy akin to that of laboratory work, the model is deliberately simplified so that the effects of reducing foliage quality on budworm-forest dynamics can be examined in isolation. My approach is deductive: using data reported in the literature and assumption when data is lacking, I mathematically describe various aspects of the budworm-forest ecosystem; then, using computer simulation, I deduce the logical consequences of these mathematical descriptions.

The Forest Submodel

The model as a whole is intended to describe the dynamic relationships between budworm density, B, foliage quantity, F, and wood volume, W, in a representative balsam fir stand in Maine. To simplify model development, I initially ignore the budworm and concentrate solely on stand growth. Although the physiology of stand growth is poorly understood, the limited evidence available suggests that the annual increments of wood volume and foliage generally increase with the rates of photosynthesis and growth hormone production (Kramer and Kozlowski 1979). Since both these physiological processes occur in the foliage and use light energy captured by the foliage (Kramer and Kozlowski 1979), the model treats foliage as the 'engine' driving stand growth.

Stands use captured light for the maintenance of existing biomass as well as for the production of new biomass. Given the lack of knowledge about how captured light is partitioned between these processes, I assume a simple linear relationship (after Smith 1963). This linearity is evident in the following description of the relative rate (U) at which the stand 'consumes' captured light in year t to t + 1:

$$U = m.F(t) + g\ [F^*(t + 1) - F(t)] \qquad (1)$$

F(t + 1) is starred to indicate that it represents the potential stand foliage quantity in year t + 1 in the absence of budworm. The coefficients m and g represent the respective rations of captured light allocated to maintenance and growth. It is implicitly assumed in this equation that foliage quantity is linearly related to stand biomass. The fact that the curvature of the relationship between wood volume and foliage quantity (Fig. 2) is small over realistic ranges suggests that this assumption may not be an unreasonable approximation. (For future reference, Table 1 alphabetically lists algebraic symbols used throughout the paper).

I also assume that in the absence of budworm, the annual 'per capita' rate of increase of stand foliage is proportional to A, the relative availability of limiting factors. It follows that the ratio of stand foliage quantities in successive years t and t + 1 can be written

$$F^*(t + 1)/F(t) = R.A + 1 \qquad (2)$$

where R is the proportionality factor, the maximum annual 'per capita' rate of foliage production possible, and F*(t + 1) is the potential stand foliage quantity in year t + 1 in the absence of budworm.

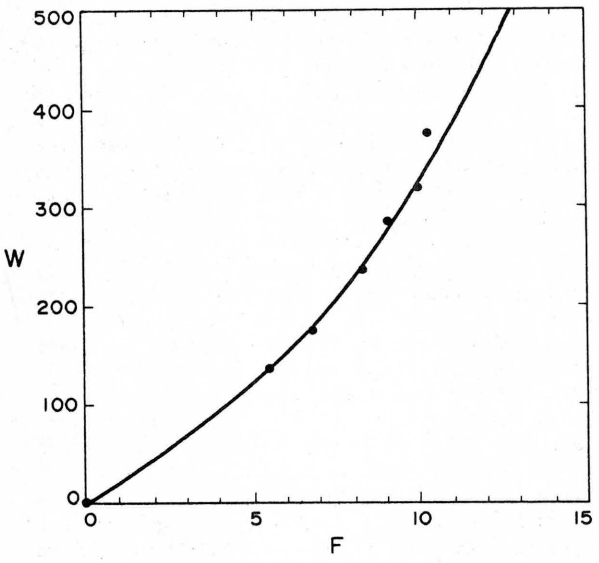

Figure 2. Wood volume, W (in m^3/ha) plotted against foliage surface, F (in 10^4 m^2/ha). Solid circles indicate the means of field observations (Baskerville, 1965, Tables 5 and 9) averaged over every 50 m^3/ha interval of W starting from W = 0. The curve illustrates equation (6).

In light-limited conditions, A can be simply expressed as

$$A = 1 - U/U_{max} \tag{3}$$

where U_{max} denotes the maximum rate at which the stand uses captured light. The existence of U_{max} follows from the existence of an upper bound on foliage quantity (Fig. 2). Hence, if F_{max} represents the maximum foliage quantity a stand can sustain, it follows from equation (1) that

$$U_{max} = m.F_{max} \tag{4}$$

Substituting equations (1) and (4) into (3), substituting the result into (2), and then rearranging, the ratio of stand foliage quantities in successive years in the absence of budworm becomes

$$\frac{F^*(t + 1)}{F(t)} = \frac{1 + R.(1 - F(t)/Fmax),}{1 + Z.F(t)} \tag{5}$$

where $Z = R.g/(m.F_{max})$. The parameter Z represents the maximum possible ration of captured light for foliage growth relative to the maximum for tree maintenance.

The economic value of a harvestable stand depends on its wood volume, and its wood volume, in turn, depends on its foliage quantity (Fig. 2). Expressing the relationship shown in Figure 2 mathematically:

$$W(t) = 544\ F(t)/[268000 - F(t)] \tag{6}$$

where wood volume, W, is measured in m^3/ha. For consistency with the rest of the paper, the units of foliage quantity in Figure 2 have been converted from the originally reported kg/ha to m^2 of foliated branch surface per ha. This conversion was accomplished by comparing Baskerville's (1965) data of F in kg/ha against W (for immature stands) with Morris' (1955, p. 287) data of F in $ft^2/acre$ in stands 35 and 55 years old. By relating stand age to W through Figure 3 and assuming that stands of equal wood volume generally have equal foliage, it was estimated that .193 kg of foliage are the equivalent of a m^2 of foliated branch surface.

Table 1. Definitions of algebraic symbols*

A	relative availability of limiting factors (-)
B	budworm density (egg masses/m^2 of foliated branch surface)
B_I	egg masses/m^2 deposited by invading moths (B)
B_N	egg masses/m^2 deposited in the stand by 'native' moths (B)
C	foliage to budworm conversion efficiency (B)
D	fraction of current foliage destroyed by budworm (-)
F	stand foliage quantity (m^2 of foliated branch surface/ha)
F_{max}	maximum stand foliage quantity possible (F)
F_s	foliage quantity of typically susceptible stands (F)
g	fraction of 'captured' light used for stand growth (1/F)
L	amount of defoliation (F)
M	annual wood volume loss through tree mortality (-)
m	fraction of 'captured' light used for tree maintenance (1/F)
n	indicates the influence of foliage on budworm ovipositioning (-)
Q	foliage quality (-)
R	maximum annual 'per capita' foliage production (-)
t	time (years)
U	relative rate by which the stand consumes captured light (-)
U_{max}	maximum value U can attain (-)
W	stand wood volume (m^3/ha)
W_M	stand wood volume when tree mortality begins (W)
W_{max}	maximum stand wood volume possible (W)
Z	ratio of the maximum possible ration of light for foliage growth relative to the maximum for tree maintenance (1/F)

* Parentheses following definitions enclose the dimensionality; e.g. 1/F indicates that g is measured in ha/m^2 of foliated branch surface and - indicates A is dimensionless.

The assumption that the data reported in Figure 3 are appropriate for a representative balsam fir stand in Maine is implicit in this conversion of foliage units. The observation that previous budworm outbreaks have left much of eastern North America's spruce/fir forest in a relatively even-aged condition (Baskerville 1976, p 8; Seymour 1980, pp 91-109) lends some support to this assumption. Whether data from a fully-stocked stand is representative is less certain.

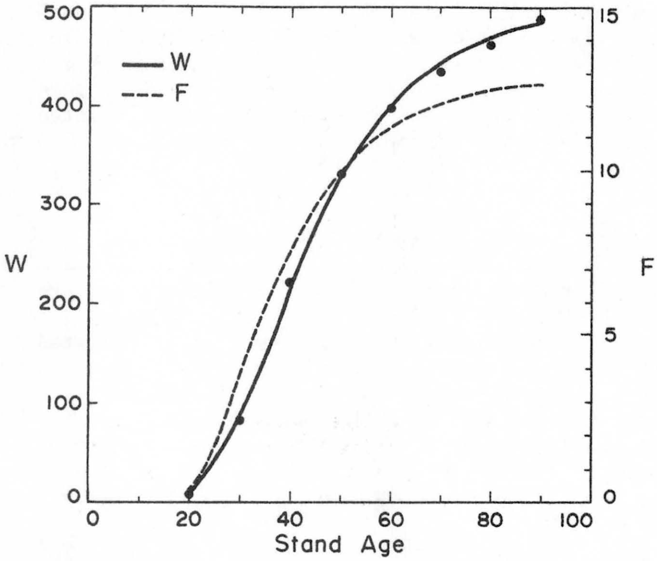

Figure 3. Wood volume, W (in m^3/ha), and foliage quantity, F (in 10^4 m^2/ha), plotted against age (years) for a fully-stocked even-aged balsam fir stand. The observations (solid circles) were taken from a good site (stand height = 18.3 m at age 65) in the northeast U.S. (Bakuzis and Hansen, 1965, Table 96). The solid and dashed lines show output of the forest dynamics submodel, equations (6) and (7), in the absence of budworm. These simulations began at t = 20 with W = 9.1.

Together, equations (5) and (6) constitute the foundation of the model's description of stand growth in the absence of budworm. A more specific description requires estimates of the parameters F_{max}, R, and Z.

Extrapolation of the field data of wood volume against stand age in Figure 3 indicates a maximum stand wood volume of about W_{max} = 500 m^3/ha. Although the physiological mechanisms limiting volume growth to $W \leqslant W_{max}$ are unknown, various observations are suggestive. First, the ratio of respiring tissue (e.g., stem cambium) to photosynthesizing tissue (foliage) increases with age (Möller et al. 1954). Second, translocation becomes more difficult as distances from the roots to the foliage increase with tree height (e.g., Kramer & Kozlowski 1979, pp 610-611). Third, mature stands generally exploit site 'carrying capacity', as reflected in light, water, and nutrient availability, more fully than very young stands (Baskerville 1965, p 2). But regardless of the physiological mechanism involved, given W_{max} = 500 m^3/ha, it follows from equation (6) that F_{max} = 128400 m^2/ha.

To estimate the parameters R and Z, numerical solutions to equation (5) with F_{max} = 128400 m^2/ha were computed for various combinations of R and Z. These solutions were translated into time series of wood volumes through equation (6) and compared to the field observations of Figure 3. A search for an acceptable series of standardized residuals (Devore 1982, p. 459-464) and a low sum of squared residuals produced estimates of R = .47 and Z = .00005 to two and one significant figures, respectively; the extra significant figure reflecting the model's greater sensitivity to R. Hence, according to equation (5), the ratio of gross (i.e., before accounting for defoliation) foliage to the previous year's net (i.e., after accounting for defoliation) foliage is

$$\frac{F^*(t + 1)}{F(t)} = \frac{1.47 - 3.6 \times 10^{-6} F(t)}{1 + .00005 F(t)} \qquad (7)$$

Figure 3 shows that in the absence of budworm, the forest submodel, equations (6) and (7), can describe wood volume growth reasonably well. However, confidence gained in the forest submodel from the results displayed in Figure 3 is limited because three parameters (R, W_{max}, and Z) were estimated from these data.

Defoliation

Completion of the forest submodel requires that the impacts of the budworm on the forest through defoliation and tree mortality be defined. Figure 4 illustrates the relationship

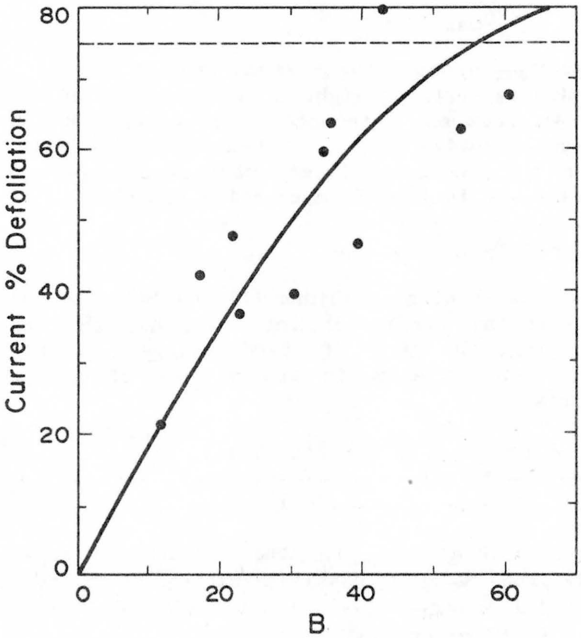

Figure 4. Plot of the % defoliation of new foliage against the number of new, healthy, budworm egg-masses per m^2 of foliated balsam fir branch surface. The solid circles show Miller's (1977, Fig. 3) data; the solid curve illustrates equation (8). Current defoliation is 75% along the dashed line.

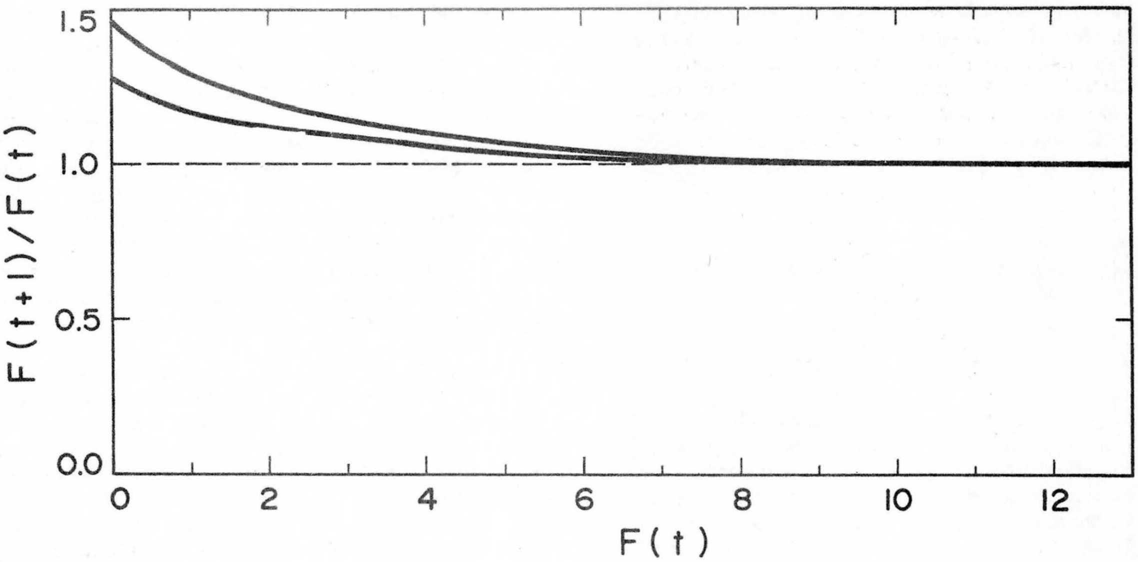

Figure 5. Foliage recruitment ratio, F(t + 1)/F(t), plotted against stand foliage quantity in year t, F(t), in 10^4 m^2/ha. The upper and lower solid curves distinguish foliage recruitment ratios for budworm densities of 0.0 and 25.8 egg-masses/m^2, respectively. F(t + 1) = F(t) along the dashed line. The curves illustrate the system of equations: (7), (9), and (10).

between current defoliation and budworm egg mass density reported by Miller (1977, Fig. 3). The curve has been visually drawn to represent his data and to pass through the origin (since no defoliation is expected without budworm). The equation

$$D(t + 1) = 1.82\ B(t)/(B(t) + 84) \qquad (8)$$

describes this curve where D(t + 1) is the fraction of current foliage destroyed in year t + 1 by budworm larvae surviving from a population of B egg-masses/m^2 in year t. Taking current foliage as F*(t + 1) - F(t), it follows from equations (7) and (8) that the total amount of foliage destroyed by budworm in year t + 1, L(t + 1), relative to the stand foliage in year t, F(t), is

$$\frac{L(t + 1)}{F(t)} = \frac{1.82\ B(t)}{B(t) + 84} \times \frac{.47 - .000054\ F(t)}{1 + .00005\ F(t)} \qquad (9)$$

Baskerville (1965, p 15) suggests .25 F*(t + 1) as an alternative measure of the amount of current foliage. The implications of this possibility are presently under investigation.

Equation (9) completes the model's description of stand foliage dynamics when tree mortality is not a factor. The model computes net foliage as a function of budworm density and net foliage in the previous year from

$$F(t + 1) = F^*(t + 1) - L(t + 1) \qquad (10)$$

where gross foliage, F*(t + 1), and losses to budworm, L(t + 1), are given by equations (7) and (9), respectively. The model then calculates W(t + 1) from equation (6), thus reflecting Peinés' (1980) conclusion that "balsam fir...growth reductions are expressed the same year as the first defoliation occurs".

Figure 5 illustrates the model's description of foliage dynamics for budworm densities of 0 and 25.8 egg-masses/m^2. This latter density represents the borderline between the 'moderate' and 'high' infestation classes of the Maine Forest Service (Fleming et al. 1983); it corresponds to 43% current defoliation (Fig. 4). The foliage recruitment ratio is a decreasing function of both foliage and budworm density.

Tree Mortality

Tree mortality usually begins after three to six years of "persistent, severe defoliation" (MacLean 1981) through some unknown physiological mechanism (Kramer and Kozlowski 1979, pp 676-677). Taking 'severe' defoliation as exceeding 75% current defoliation (after Baskerville and MacLean 1979), the model triggers the tree mortality process in the fifth consecutive year of budworm densities above 58.9 egg-masses/m^2 (the density corresponding to 75% current defoliation in Fig. 4).

Once tree mortality begins, foliage is no longer the 'engine' driving wood production. Rather, the model reduces total stand foliage roughly in proportion to, and as a consequence of, losses in W, the wood volume contributed by live trees. (Since W excludes wood volume contributed by dead trees, using W to indicate stand value ignores any possible profit from salvage operations.)

If M is the fractional loss of wood due to tree mortality in any year while tree mortality is occurring, then the fractional survival rate is 1-M. Therefore, since tree mortality continues for six consecutive years in a representative stand (MacLean 1981, Fig. 1), stand wood volume at the completion of tree mortality is

$$W(t_M + 6) = (1-M)^6 W(t_M)$$

where t_M is the year when mortality began. Algebraic manipulation of this equation shows that

$$M = 1 - \exp(.167 \ln[W(t_M + 6)/W(t_M)]).$$

MacLean (1981, Fig. 1) suggests that once triggered, cumulative tree mortality (in number of stems) reaches about 99% in mature stands and 55% in immature stands after six years. Since mortality in number of stems generally provides a reasonable approximation to mortality in wood volume (MacLean 1980), it follows from the equation above that M = .54 and .12 for mature and immature stands, respectively. Wood volumes corresponding to mature and immature stands were estimated from Baskerville and MacLean (1979, Table 7) as 450 m^3/ha and 135 m^3/ha, respectively. Thus the model can use stand wood volume at the onset of tree mortality, W_M, as an indicator of stand age. A simple expression fitting these observations and the constraint that M = 0 when $W_M = 0$ is

$$M = 10^{-6} W_M^2 + .00075 W_M. \qquad (11)$$

Summarizing, the model's tree mortality process begins in the fifth consecutive year of budworm densities exceeding 58.9 egg-masses/m^2 and continues for six years causing an annual volume loss of M x W. The model treats the fractional loss of wood volume due to tree mortality, M, as a function of the stand's wood volume when tree mortality started, W_M. While tree mortality is occurring, foliage is calculated through the inverse of equation (6).

The Budworm Submodel

Although the spruce budworm - forest system has periodically been the object of intensive investigation, many questions remain to be answered regarding the reciprocal impacts between the budworm and its hosts. These uncertainties are necessarily reflected in the following submodel of budworm dynamics. This submodel is meant to provide a simple qualitative description of budworm population dynamics: it can claim to be neither definitive nor quantitatively accurate. Nonetheless, it will provide a useful basis for discussing the qualitative impacts of changes in foliage quality.

The development of the budworm submodel begins by distinguishing between the eggs laid by moths invading the stand and those 'native' to the stand. If B is the budworm density (in egg masses/m^2 of foliated branch surface) then the annual change in budworm density is

$$B(t + 1) - B(t) = B_N + B_I - B(t) \qquad (12)$$

where B_N and B_I are the egg masses/m^2 deposited in the stand by budworm which developed within and outside the stand, respectively. Thus B_N and B_I represent the egg deposition in the stand by 'native' and invading moths. The last term on the right side of equation (12) represents budworm mortality. Its form reflects the maximum budworm longevity of about 13 months: local extinction must exist, at least temporarily, following a complete lack of ovipositing within the stand (i.e., when $B_N = B_I = 0$).

Indirect evidence (Greenbank et al. 1980; Miller 1979; Morris 1963) suggests that dispersing moths favor stands with many large, mature, well-foliated balsam fir trees for oviposition. Miller et al. (1978) estimated that moths invading a heavily sprayed test block from the surrounding infested forest deposited about 10 masses/m^2. But budworm are reportedly rare between outbreaks (Baskerville 1976; Morris et al 1958) so B_I is likely small in most stands lacking suitable foliage. Accommodating these assumptions and observations, the budworm immigration density can be expressed as an exponentially increasing function of foliage quantity:

$$B_I(t) = 10[F(t)/F_s]^n$$

where F_s represents the foliage quantity in a typical susceptible stand and n is a yet to be determined exponent indicating how abruptly immigration increases with increases in stand foliage.

Balch (1946) reports that moderately and highly susceptible stands generally exceed 40 and 60 years of age, respectively. Accepting the mean age of 50 years, the model assigns typically susceptible stands an average foliage quantity of $F_s = 10^5$ m^2/ha in accordance with Figure 3. Then, given respective practical maximums for F and B_I of 1.2 x 10^5 m^2/ha (Fig. 2) and 20-30 egg masses/m^2 (Miller et al. 1978), n = 5 to the nearest integer satisfies the expression for B_I above. Hence, the annual egg mass deposition by invading moths becomes

$$B_I(t) = 10 [F(t)/10^5]^5 \qquad (13)$$

The density of egg masses deposited by native moths, $B_N(t)$, also depends on stand foliage, F(t). Assuming the total number of eggs deposited by native moths in year t, $B_N(t)$ x F(t), is proportional to the foliage consumed, L(t),

$$B_N(t) = C.L(t)/F(t)$$

where C is the foliage to budworm conversion efficiency (i.e., the egg masses produced per m^2 of foliated branch surface destroyed). Since larval survival and moth fecundity reportedly increase as stand maturity increases (Morris et al. 1958; Morris 1963, p 189-202), and since moth fecundity declines exponentially as the duration of sustained severe defoliation increases (Morris

1963, pp 85-87), C is likely an increasing function of foliage. A simple possibility is

$$C = Q[F(t)/F_s]^n$$

where Q represents foliage quality in terms of budworm reproductivity and n is an unspecified exponent determining how sharply C accelerates as F(t) increases. Combining the last two equations, and recalling that the amount of foliage of typical susceptible stands is $F_s = 10^5$ m^2/ha, the annual egg mass deposit by native moths becomes

$$B_N(t) = Q.L(t).F(t)^{n-1}/10^{5n} \qquad (14)$$

Equation (14) completes the model: equations (12), (13), and (14) constitute the budworm dynamics submodel; equation (11) describes the tree mortality process; equations (7), (8), and (9) link the budworm and forest submodels through defoliation, and equations (5) and (6) comprise the forest growth submodel.

Values for n and Q, however, remain undetermined in equation (14). Simulations of the complete model with initial conditions W = 9.1 m^3/ha (Fig. 3), F = 4409 m^2/ha [equation (6)], and B = B_I = 1.7 x 10^{-6} masses/m^2 [equation (13)] and with various values of n and Q displayed a variety of different outbreak cycles. Realistic cycles are generally 26-40 years in length (Royama 1982) with outbreaks lasting 6-15 years in relatively unmanaged forests (Baskerville 1976; Stedinger 1977) and with budworm densities varying over four orders of magnitude (Baskerville 1976). Since Q = .06 and n = 5 produced the cycles which best met these criteria and which had a realistic range (c.f. Fleming et al. 1983) of budworm egg mass densities, these values were adopted as reference points for other simulations.

Model behavior, however, may also be acceptable for very different values of n and Q. Nonetheless, this is unlikely to affect the range of qualitative behavior exhibited by the model as Q varies: the model is behaviorally consistent for changes in n (excluding n values which do not admit acceptable outbreak behavior). Therefore, since this paper deals only with the qualitative behavior of the model, such behavior will be discussed only for n = 5 below.

A final comment on the form of equation (14) - the function $B_N(t)$ represents the product of the survival of the local population from eggs in year t-1 to moths in year t times the local reproductivity of those moths. Moreover, the (generation) survival component of $B_N(t)$ is itself the product of the survival rates for each of the six larval instars. Hence, since many of these instar survival rates probably increase with foliage (Thomson 1979), there is some theoretical basis for writing $B_N(t)$ as a function of F(t) raised as high as the fourth power.

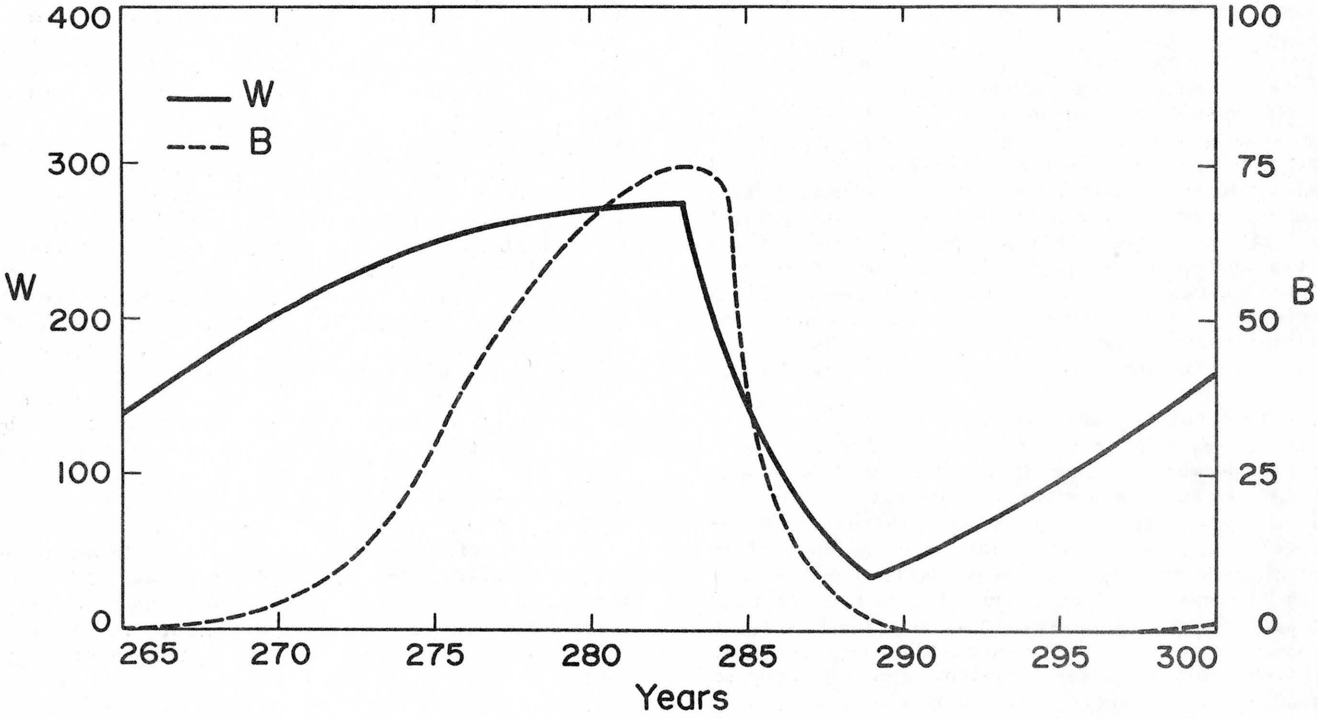

Figure 6. The 33-year outbreak cycle produced by the full model under 'natural' foliage quality conditions (i.e., Q = .06). Wood volume, W, and budworm density, B, are shown for years 265-300 of a numerical solution to equations (5)-(9), (11)-(14) with n = 5. The simulation began in year 20 with W = 9.1 m^3/ha and B = 1.7 x 10^{-6} egg-masses/m^2.

Model Behavior

Figure 6 illustrates the behavior of the model through a typical outbreak cycle. Beginning at t = 265, both budworm density (B) and foliage increase with time, changes in foliage being reflected (through Fig. 2) by the wood volume (W) curve in Figure 6. Foliage increases favor the budworm population [cf. equations (12)-(14)] which grows in response. But as it grows it destroys more foliage (Fig. 4), thus reducing the foliage and volume increments. By t = 280 the budworm population has become so large (over 58.9 masses/m^2) that current defoliation exceeds 75% [equation (8)]. Tree mortality, equation (11), begins in the fifth consecutive year (t = 284) of such severe defoliation and decimates the wood volume and foliage during the next six years. The budworm population crashes in response to the consequent loss of feeding and oviposition sites. By t = 289 most of the overstory has been destroyed (low W) and the immature, relatively less vulnerable understory trees are beginning stand regeneration.

When foliage quality, Q, is reduced 50% from its value of .06 in Figure 6, (and nothing else is changed), the model exhibits a very different behavior: the outbreak cycles are replaced by a state of apparent equilibrium with the budworm density, B, stable at 35 masses/m^2 and the wood volume stable at its maximum of 500 m^3/ha. Curiously, this reduction of foliage quality allows both the budworm and the wood volume to maintain greater long term averages than they did in Figure 6: the budworm density does not get high enough for long enough to trigger the tree mortality process. The reduction in foliage quality acts to slow budworm increase during its population growth phase (265 < t < 280 in Fig. 6) and this prevents prolonged severe defoliation before the budworm population declines in response to reduced foliage levels. Hence, tree mortality seems necessary for the model to exhibit outbreak cycles; this is the basis of the tree mortality hypothesis of outbreak generation.

The foregoing analysis deserves two qualifications. First, stands don't last forever even without budworm: they deteriorate with age and become susceptible to fire, diseases, and other pests. Hence, the 'apparent equilibrium' is more properly viewed as a long-term regeneration cycle; budworm-caused tree mortality short-circuits the cycle. Second, model behavior is not independent of its starting point: for particular values of Q (n = 5) the model could exhibit both outbreak cycles and apparent equilibria depending on the initial conditions. These qualifications also apply to Table 2.

Table 2 summarizes the results of model simulations beginning at t = 20 with W = 9.1 m^3/ha and B = B_I = 1.7 x 10^{-6} masses/m^2 for various values of Q. (Figs. 3 and 6 correspond to the runs for Q = .0^3 and .06, respectively.) Reducing foliage quality (Q) has a number of benefits for the forest manager: increasing peak wood volume, decreasing peak budworm densities, and lengthening the outbreak cycle period (realistically, steady states represent long-term regeneration cycles). Reducing foliage quality can also have detrimental effects. First, it lengthens outbreak duration (defined as the period during which B > 25.8 masses/m^2) although this effect is usually small and not in proportion to the period lengthening. Second, tree mortality is more severe as a consequence of the greater maximum wood volumes [equation (11)]. However, further reductions of foliage quality (e.g., Q < .03 in Table 1) can prevent budworm outbreaks from occurring at all. Hence, the major consistent effects of reducing foliage quality in this model are increases in maximum wood volume and decreases in budworm outbreak frequency.

Table 2. The effect of foliage quality on model behavior.

Foliage Quality (Q)	Outbreak Cycle Period (years)	B[1] (masses/m^2)	W[1] (m^3/ha)
.6	19	225.1	163.1
.1	27	98.46	236.6
.065	32	78.55	267.9
.06	33	75.00	274.5
.055	35	72.81	283.4
.05	37	69.79	293.3
.045	40	67.25	306.0
.04	44	64.41	322.1
.035	52	62.43	347.1
.03	55[2]	58.66	398.2
.01	55[2]	32.31	449.1
.0	55[2]	27.71	458.7
.0[3]	55[2]	0[3]	484.6[3]

[1] B and W columns list the outbreak cycle maximums when Q ⩾ .035 and the 90-year values when Q ⩽ .03.

[2] Quasi steady state behavior - no outbreaks.

[3] No budworm immigration (i.e., B_I = 0).

Other Hypotheses of Outbreak Generation

The models underlying various outbreak hypotheses are conveniently compared in terms of recruitment ratios, the ratios of budworm densities in successive years in the absence of moth immigration. For instance, according to equations (12)-(14), $B_N(t)/B(t)$ approximates the recruitment ratio for the tree mortality model. Curves a and b of Figure 7 show that this ratio increases with stand foliage and decreases with budworm density. Curve b shows that when the stand is immature (F = 70000 m^2/ha), $B(t + 1)/B(t) < 1$ so the native budworm population declines steadily. But as the stand matures (F increases) the recruitment rate rises until $B(t + 1) > B(t)$ at small densities (e.g., curve a). The native population can then increase up to its equilibrium density (the density at which the recruitment curve crosses the dashed line); for curve a, 68 masses/m^2. At densities above and

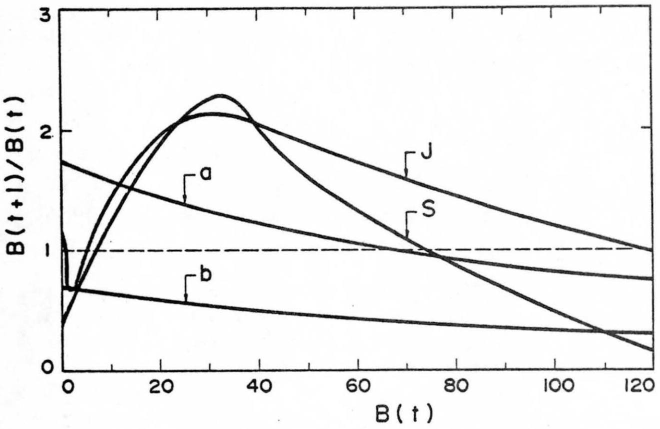

Figure 7. Budworm recruitment ratios, $B(t + 1)/B(t)$, when immigration is negligible plotted against budworm density in year t, $B(t)$, in egg-masses/m^2. Curves a and b distinguish ratios for foliage quantities of 90000 and 70000 m^2/ha, respectively, in the model developed above. Curves J and S respectively represent ratios for Jones' (1979) and Stedinger's (1977) models. Equilibria occur wherever the curves cross the dashed line, $B(t + 1) = B(t)$.

below this equilibrium the population decreases and increases, respectively. Hence, the equilibrium is stable: any slight deviation from the equilibrium density will be followed by a return to it.

Curve S in Fig. 7 typifies recruitment ratios for Stedinger's (1977) model; equilibria occur at 6 masses/m^2 and 74 masses/m^2. The lower one is unstable: slightly smaller densities lead to continued decrease, slightly larger ones to continued increase. Hence, in Stedinger's model, a sparse population cannot grow of its own accord: moth invasion is needed to raise the budworm density above the unstable equilibrium density, in which case, an outbreak is inevitable.

Curve J in Figure 7 illustrates the budworm recruitment curve in a stand with moderately favorable conditions in Jones' (1979) model. Stable equilibria occur at 1 and 118 masses/m^2 and an unstable equilibrium occurs at 5 masses/m^2. However, as in the tree mortality model, stand conditions determine the elevation of the entire curve. When the dip in the recruitment curve at low densities eventually clears the dashed line in response to improved stand conditions, the two lower equilibria vanish allowing the budworm to increase quickly to outbreak densities. The resulting forest destruction is reflected in the drop of the entire curve below the dashed equilibrium line and this signals the ensuing collapse of the budworm population. Subsequent stand regeneration causes the slow elevation of the budworm recruitment curve but the next outbreak does not occur until the dip at low densities has again cleared the dashed equilibrium line.

Although stochasticities introduced by weather and moth invasion also play a role, it is clear that the low density dip, the so-called 'predator pit', dominates the behavior of Jones' model. The predator pit represents the assumed effect of a group of background natural enemies (principally birds) whose relatively small reproductive potential prevents their populations from keeping pace with budworm increases during outbreaks. This predator pit is the basis for the slow enemies hypothesis of outbreak generation attributed to Baskerville (1976) and Jones (1979) in Figure 1.

Reducing foliage quality has similar effects on the qualitative dynamics of each of the models discussed in detail above. Equation (14) shows that foliage quality, Q, determines the height of the recruitment curve, $B_N/B(t)$, at any given budworm density for the tree mortality model. Hence, for given forest conditions and budworm densities, decreasing foliage quality lowers the height of the recruitment curve and hence reduces the propensity for budworm increase. The result is a reduction of the frequency and severity of outbreaks (Table 2). Analogously, reducing foliage quality can be expected to lower recruitment curves (Fig. 7) for both Stedingers' model and Jones' model. Consequently, more immigrant moths would be needed to trigger an outbreak in Stedingers' model and greater stand maturity (larger F values) would be needed to overcome the effect of the predator pit and initiate an outbreak in Jones' model. Hence, for both these models, reducing foliage quality can be expected to reduce budworm outbreak frequencies and increase maximum wood volumes. But, since tree mortality increases with maximum wood volume, reducing foliage quality and thus extending the period between outbreaks results in greater stand destruction when outbreaks do occur (see also Casti, 1982).

The effects of reducing foliage quality are less certain for the fast enemies hypothesis of budworm outbreak generation. According to this hypothesis, certain budworm parasitoid and pathogen populations increase so fast in response to increased budworm densities during outbreaks that they subsequently decimate the budworm populations, thus ending the outbreaks. The complexity of such a system and the uncertainties regarding the attributes of the mortality factors make it particularly difficult to predict how it will respond to reductions in foliage quality. Nonetheless, given these reservations, longer intervals between outbreaks, greater wood supplies, and more severe outbreaks can be expected in the short-term. However, in the long-term, reducing foliage quality may have some undesirable effects. For instance, parasitoid and pathogen populations which lack sufficient alternate hosts and are unable to maintain their populations on low budworm populations during the longer intervals between outbreaks may become exceedingly rare. Thus freed of these parasitoids and pathogens, the budworm might become an even greater pest than it had been before foliage quality was reduced.

Summary and Conclusions

The consequences of reducing foliage quality on spruce budworm dynamics have been discussed for four hypotheses of outbreak generation (Fig. 1). These hypotheses differed with respect to the principle biological mechanism underlying budworm outbreaks: tree mortality (Blais, 1974), slow natural enemies (Baskerville 1976; Jones 1979), fast natural enemies (adapted from Royama 1982), and moth invasion (Stedinger 1977). Despite these differences, the analysis indicated that the immediate consequences of reducing foliage quality should be similar for each hypothesis: increasing maximum wood volume, decreasing outbreak frequency, and increasing outbreak severity. The first two consequences offer benefits for forest management: increasing maximum wood volume implies an increase in the economic value of the stand at cutting time; decreasing outbreak frequency implies that a stand need be cut less often to preclude budworm-caused tree mortality, and therefore that the economic costs of harvesting could be reduced.

In the long-term it is clear that the budworm would face extinction given sufficient reduction of foliage quality. More modest and more realistic expectations for foliage quality reductions would have the budworm always present. The long-term consequences should then be similar to the short-term consequences for each hypothesis with two possible exceptions. First, if some of the fast natural enemies cannot maintain viable populations during the longer intervals between budworm outbreaks, short-term 'improvement' of the budworm problem may be followed by its long-term 'aggravation': greater outbreak frequency and smaller maximum wood volumes. Second, the possibility of genetic adaptation by the budworm to changes in foliage quality has not been considered. Suffice it to say that the budworm, with a one year generation time, appears to have the potential to adapt quickly enough to cause problems. Perhaps agriculture can suggest a solution to this potential problem: cultivar mixtures, multilines, and horizontal resistance (e.g., Fleming and Person 1978, 1982) have each been proposed as means of incorporating crop resistance against short-generation plant pathogens.

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CHARACTERISTICS OF STANDS SUSCEPTIBLE AND RESISTANT TO GYPSY MOTH DEFOLIATION

David R. Houston

Principal Plant Pathologist, USDA Forest Service, Northeastern Forest Experiment Station, Center for Biological Control of Northeastern Forest Insects and Diseases, 51 Mill Pond Road, Hamden, CT 06514

Site conditions strongly influence where gypsy moth defoliation will occur. In New England, where gypsy moths and forests have interacted for over a century, some forests have had a history of repeated defoliation while others have been defoliated only rarely. The often defoliated or susceptible forests characteristically grow on dry sites such as rocky ridges or deep sands. In many cases, they have been disturbed--sometimes frequently--by fire, wind, snow, or ice storms. The trees in these forests, mainly dry-site oaks, often are highly favored as food by gypsy moths, are slow growing, small, and scrubby, and have abundant structural features such as bark flaps, deep bark fissures, and holes or wounds that are used as resting sites by gypsy moths.

The open nature of susceptible forests encourages the growth of plants such as blueberry, huckleberry, bracken, sweetfern, grasses, and sedges. Leaf litter usually is shallow or lacking; on ridge stands, surface rocks or exposed ledges are common.

Resistant forests where defoliation is rare characteristically grow on relatively undisturbed sites with well-drained, deep loam soils where moisture is not limiting. They usually are well stocked and contain mixtures of species, including some that are highly preferred. Trees on these sites have good growth rates and relatively few structural features used by gypsy moths.

Understory plants in New England's resistant forests include such species as wild sarsaparilla, maple-leafed viburnum, and woodland ferns. Resistant stands have deep litter layers that are favorable habitat for many predators of gypsy moth.

It is not axiomatic that trees growing on susceptible sites are more apt to succumb to a given defoliation regimen than trees on resistant sites. Studies suggest that trees on adverse sites may be no more--indeed, may even be less vulnerable--than trees on good sites. Perhaps this reflects, at least in part, the fact that trees on poor sites represent the survivors of an exceptionally intense and continual selection process. Other relationships that are probably involved include the relative energy demands of small, slow-growing trees compared to large fast-growing ones; the amounts and conditions of substrates that support fungi and insects that attack and kill defoliation-stressed trees.

These descriptions of susceptible and resistant stands in the Northeast represent the extremes of a range of susceptibilities. It is likely that stands will be susceptible if they are on adverse sites and contain high proportions of preferred tree species with abundant refuges. It is also likely that well-stocked, mixed, fast-growing stands free of recent disturbance will be resistant, and will suffer damaging defoliation only upon disturbance or upon invasion by a large number of larvae from adjacent areas.

But stands at opposite ends of the susceptibility spectrum are not always, indeed not usually, encountered. In New England, many intermediate stands on mesic sites are changing from susceptible to resistant as their natural development is accompanied by decreases of highly preferred species and by proportionate increases of less preferred species. Intermediate stands that contain sizable proportions of highly preferred food species can be rendered more susceptible by disturbances that "open them up" and favor once again the more light-demanding food species that are preferred by the gypsy moth. Such disturbance also can reduce the impact of ground-inhabiting gypsy moth predators by removing or drying out the litter and soil habitat so important to these animals' survival and by creating above-ground protective refuges for the insect on the trees.

We often refer to susceptible stands, particularly those on ridges, as focal sites, and research and observations have indicated that gypsy moths do spread from such stands to surrounding more resistant forests. Probably susceptible stands should also be considered as focal areas for the processes that contribute to release of gypsy moth populations. Conceptually, susceptible stands that are under more or less continuous moisture stress and disturbance support the systems for population release that are expressed in more "buffered" resistant forests following periods of water shortage or disturbance.

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MANAGEMENT IMPLICATIONS OF INTERACTIONS BETWEEN THE SPRUCE BUDWORM AND SPRUCE-FIR STANDS

John A. Witter, Ann M. Lynch, and Bruce A. Montgomery

Associate Professor, Graduate Research Assistant, and Coordinator of the Spruce Budworm Technology Transfer Program, respectively.
The University of Michigan
School of Natural Resources
Ann Arbor, MI 48109

Abstract. The impact of the budworm on trees and stands and conditions that lead to susceptible and vulnerable stands are discussed. Long-term and short-term options dealing with the spruce budworm problem are presented. Examples of questions that plant-animal interaction research have answered are presented in the following scenarios: (1) can the release phase of an outbreak be detected, (2) can spruce budworm impact be predicted, (3) are regionwide rating systems accurate, and (4) what, if any, relationships exist between site classification units and spruce budworm impact.

Introduction

The North American boreal forests have experienced periodic spruce budworm outbreaks for hundreds of years. Although the spruce budworm is an integral component of spruce-fir forests in North America, it normally does not prevent the continuity of spruce-fir forests. Fir and spruce usually regenerate after an outbreak, reaching a merchantable size in 40 to 60 years.

The spruce budworm was not considered a major problem in eastern North America until 40 years ago. Expansion and addition of numerous pulp and paper mills led to greater market demand for spruce and fir. More intensive forest management practices were needed to meet this demand and to reduce the amount of impact of the spruce budworm on spruce-fir stands. These practices had to be based on a thorough understanding of the interactions between budworms and forests under a variety of management scenarios.

As researchers, we understand the value of basic studies involving plant-animal interactions in forest ecosystems. However, we have not done a very good job in justifying this kind of research to the applied forestry community. Hopefully, this paper and others presented at this workshop will help show how both basic and applied studies on plant-animal interactions are vital if we are going to provide the land manager with sound forest pest management programs. This paper is divided into three sections: biological information, management options, and interesting scenarios involving plant-animal interactions.

Biological Information

Insect impact is any effect that insect activity has on a forest resource. Impact can be described as having a positive effect, negative effect, or no effect. Damage implies a harmful or negative effect. Land managers are usually interested in the evaluation of this negative effect.

The interaction between the spruce budworm and the spruce-fir forest involves the effect of the budworm on the forest and the effect of the forest on the budworm. The terms susceptibility and vulnerability have been applied to these interactions. Susceptibility is the probability that a stand will be attacked by the budworm. Vulnerability is the probability of tree mortality in the stand once a budworm attack occurs. In this section, we describe the impact of the budworm on trees and stands and conditions that lead to susceptible and vulnerable stands.

Impact on Trees and Stands

Budworm impact includes growth loss, cone and seed mortality, top-kill, tree and stand mortality, changes in stand composition, and various interactions between the budworm and other organisms in the forest (Table 1). Studies on growth loss in North America have shown a 30 to 90 percent reduction in radial growth in spruce-fir stands heavily defoliated by the spruce budworm for 2 to 6 years (MacLean 1981). A considerable increase in balsam fir cone and seed mortality occurs during an outbreak; few sound seeds are produced during a severe outbreak (Hudak and Raske 1981). Top-kill usually begins during the third year of an outbreak. The total number of dead tops often reaches 50 percent or more. Fir trees in the codominant and dominant crown classes usually die after about 5 years of repeated defoliation of current year's growth. Complete stand mortality can occur after 7 to 10 years of continuous heavy defoliation. Mortality in mature fir stands usually ranges from 70 to 100 percent, while mortality in immature stands varies from 30 to 70 percent (MacLean 1980). Budworm attack can result in changes in stand composition (Ghent et al. 1957, Turner 1952). However, spruce budworm destroyed forests usually regenerate with spruce and fir. Repeated removal of current year's needles by the budworm results in reduced tree vigor and subsequently makes the trees more susceptible to bark beetles and fungi (Basham and Belyea 1960, Belyea 1952). The impact of spruce budworm attack may be transitory or long-lasting (Batzer 1969, Blais 1958).

Conditions Leading to Susceptible and Vulnerable Stands

Any spruce-fir stand or host tree in eastern North America is susceptible to a spruce outbreak. As a general rule, certain factors usually increase the amount of volume loss and tree mortality in a spruce-fir stand during a

Table 1. Succession of events associated with a spruce budworm outbreak, on balsam fir (modified from Montgomery et al. 1982).

Years of severe defoliation[a]	Impact
1	Flowers and cone crops die. Radial growth loss occurs in the upper crown.
2 to 3	Small roots begin to die. Radial growth loss occurs over the entire stem. Height growth ceases. Some treetops die.
4 to 6	Suppressed trees in the understory and mature and overmature trees in the overstory begin to die. Tree growth and wood production nearly ceases.
7 to 15	Budworm populations begin to collapse. More trees die, particularly balsam fir. Some seedlings and saplings die. Dead trees begin to deteriorate as a result of disease, secondary insect attack, and wind breakage. Protective cover in deer yards is diminished.

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[a] 75 percent or more of current year's growth.

Table 2. Factors that increase the amount of damage (volume loss and tree mortality) in a spruce-fir stand (from Witter et al. 1983).

General factor	Conditions leading to severe damage
Intensity and duration of outbreak	Stand mortality usually increases with the severity and length of outbreak.
Species composition	Stands with large balsam fir components have greater potential for mortality than stands comprised mostly of spruce and hardwoods.
Stand age	Mature fir stand (60 years or older)
Stand density	High basal area of balsam fir, red spruce, and white spruce
Stand structure	Open stands in which spike tops of host species protrude from forest canopy
Site condition	Poorly drained stands, abnormally dry or wet
Stand size	Extensive stands of mature host trees (except black spruce)
Stand location	Stands located downwind (often east) of the current outbreak
Topography and latitude	Stands growing at elevations lower than 2300 ft (700 m) and south of 50° latitude

budworm outbreak (Table 2). Stand mortality usually increases with the duration and severity of the outbreak. Percent tree mortality is greatest in stands with the highest proportion of balsam fir followed in descending order by white, red, and black spruce. Mortality is usually much higher in stands greater than 60 years old. Open stands in which spike tops of host trees protrude from the forest canopy often suffer more damage. Stands on abnormally dry or wet sites usually sustain more damage.

The factors presented in Table 2 usually hold true, but there is great variation within the boreal forest (Mog et al. 1982, Blais 1968). For more information, Witter et al. (1983) presented a detailed review on the impact of the budworm on trees and stands.

Management Options

From a land manager's perspective, nothing can be done to prevent or control a regional outbreak of the spruce budworm since management actions are directed at individual stands (Simmons et al. 1983). There are three types of options available to the land manager: (1) actions directed at the stand (i.e., silvicultural techniques), (2) actions directed at the budworm (i.e., microbial or chemical insecticides), or (3) no action. None of these management options will result in the control of a regional outbreak.

The land manager can influence the time, place, and quantity of mortality that will occur in his or her forest. Various intensive forest management practices reduce spruce-fir vulnerability by replacing budworm-prone forests with less susceptible forest types. The following recommendations are good long-term goals (Flexner et al. 1983):

(1) Shorten the rotation age of fir to 50 years or less.
(2) Break up the continuity of extensive areas of mature forest.
(3) Maintain a mixed-species composition whenever feasible.

(4) Convert the stand to less susceptible species.
(5) On a regional basis, optimize the spatial diversity of different even-aged stands.

Research on plant-animal interactions will help us to plan better forest management approaches for reducing future budworm impact. However, even the best approach will never prevent budworm outbreaks.

Once an outbreak occurs, short-term options available to help protect or to harvest the trees in the most seriously threatened stands are salvage operations and spraying valuable stands with microbial or chemical insecticides.

Using biological information, the land manager can rank the probability of damage to his or her stands. Salvage operations can be conducted first in the highest risk stands. A land manager may decide to spray an insecticide in the most valuable mature spruce-fir stands that are heavily attacked by the budworm and may die within a few years. If markets are poor, the land manager may choose to abandon the stand.

Interesting Scenarios Involving Plant-Animal Interactions

Current studies are helping land managers and researchers to better understand interactions between the budworm and spruce-fir forests. These studies have and will continue to produce techniques to reduce the amount of budworm-prone forests and to provide more environmentally sound techniques to reduce the impact of the budworm on the forest. Four scenarios are presented to show the examples of some of the questions that research on plant-animal interactions have answered or are trying to answer.

Scenario 1: The Release Phase Of An Outbreak Can Be Detected -- Yes, No, Maybe

In studying the current outbreak in Quebec, Hardy et al. (1983) found that the outbreak started in seven epicenters. All were located in mixed-wood stands that included sugar maple, yellow birch, and white pine. Softwoods, about 50 years of age, occupied less than 30 percent of the stand. Ecological disturbances such as fire and logging occurred in all epicenters. The outbreak was first detected in areas with few balsam fir. Also, the major front of the outbreak was preceded by the establishment of a number of infestation centers distributed in an east-west pattern. If we can locate epicenters, early detection of incipient outbreaks may make modification of management plans possible.

An understanding of where epicenters may occur could be helpful to pest management specialists responsible for monitoring budworm populations. The use of a pheromone sampling system to monitor low population levels of the spruce budworm is now feasible (Allen and Dorais 1983). The pheromone sampling system is currently being pilot-tested in eastern North America. This type of sampling system, when it becomes operational, will allow a land manager to detect an increase in the budworm population as many as five years prior to noticeable defoliation.

Scenario 2: Spruce Budworm Impact Can Be Predicted -- Yes, No, Maybe

Land managers must be able to predict the type and amount of damage from the budworm to effectively manage their stands. A number of rating systems (both short-term and long-term) have been developed to assist the forest manager in determining the vulnerability of the forest to budworm attack (McCarthy et al. 1983, 1982; Blais 1975; Batzer 1973, 1969; Graham 1956; Bean and Batzer 1956; Westveld 1954, 1945; Morris and Bishop 1951; McLintock 1948, 1949; Balch 1946). Budworm impact can be predicted.

Many of the rating systems currently in use in eastern North America concentrate on short-term objectives. These rating systems are used to help managers determine which stands need to be salvaged or sprayed during the next year or two.

An example of a short-term rating system using 35mm aerial photographs is described by Olson et al. 1982. This system is based on the proportion of host species within the stand, average tree condition ranking for the stand, and the existing percent mortality of host species. The land manager uses the stand-rating mortality of host species. The land manager uses the stand-rating value for each stand to plan which stands should be salvaged or protected during the next several years. The system also has been adapted and used with a 70mm camera system.

Long-term rating systems are based on the concept of vulnerability and are used to help the land manager reduce the vulnerability of the forest over time. Lynch, Fowler, and Witter developed a long-term rating system for Michigan's Upper Peninsula to predict the amount of balsam fir basal area per hectare that will die due to the budworm. Factors which influenced budworm impact in the Upper Peninsula were: (1) the length of time the outbreak has been in progress in different parts of the Peninsula, (2) the quantity of balsam fir present in the stand, (3) stand species composition, (4) site factors, particularly drainage, and (5) past and present land management practices. This rating system will provide the land manager in the Upper Peninsula of Michigan with a useful management tool by estimating potential losses. The estimates can be used to plan preventive, presalvage, and salvage harvesting programs. The system can be easily implemented by land managers because the necessary data are readily available from routine compartment examinations and inventory systems.

Scenario 3: Regional-Wide Rating Systems Are Accurate -- Yes, No, Maybe

The rating systems developed so far do not have high predictive accuracy throughout the insect's entire range or have not been tested over the insect's entire range. However, a rating system developed to help the land manager determine the vulnerability of the forest to budworm attack at the management unit level in eastern Canada is compatible for both New Brunswick and Quebec (MacLean 1982, Blais and Archambault 1982). Their vulnerability index provides a rating based on the combined volume of balsam fir and white spruce, combined volume of black and red spruce, the maturity of balsam fir, and climate. This system depends on the availability of forest inventory data and is not fully operational at this time. Long-term rating systems in the Great Lakes Region do not appear to be compatible over the entire Region. For example, Lynch, Witter, and Fowler had to use five models to predict the amount of balsam fir basal area per hectare that will die due to the spruce budworm in the Upper Peninsula of Michigan. Their system differs from the system developed by Batzer and Hastings (1981) for Minnesota. The answer to the question on whether region-wide rating systems are accurate appears to vary by region. The land manager must be very careful about using any rating system that has not been validated for his or her area.

Scenario 4: There Is A Relationship Between Site Classificiation Units and Impact From The Spruce Budworm -- Yes, No, Maybe

Stand mortality is not evenly distributed within a state or province. These differences may be partially due to site conditions. A number of site classification systems are currently being developed in North America. A logical approach is to break an area into ecosystem units that are consistently found in the stand. These ecosystem units can be distinguished by differences in physiography, soils, and vegetation (Barnes et al. 1982). Individual characteristics such as topography, drainage, aspect, slope, depth of organic matter, soil pH and tecture, and plant species groups may be incorporated into a site classification scheme. Hix et al. (1983) developed a classification system for spruce-fir stands in the Ottawa National Forest in Michigan's Upper Peninsula based on site and vegetative characteristics. Currently, the possible relationships between site classification units and damage is being analyzed. This type of study helps determine if there are relationships between sites, the budworm, and damage.

Final Discussion

If we are going to manage the forest in a way that is both ecologically sound and financially rewarding, a thorough understanding of the interactions between the budworm, site conditions, and stands is necessary. Progress has been made during the last decade in building a knowledge base as shown by the scenarios in this paper and in the other papers presented at this workshop. The implementation of this knowledge base has already resulted in improved management decisions. We must continue to support long-term studies on plant-animal interactions in order to further improve our knowledge base and decision making abilities.

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BIOMASS AND NITROGEN BUDGETS DURING LARVAL DEVELOPMENT OF *LYMANTRIA DISPAR* AND *CHORISTONEURA FUMIFERANA*: ALLOMETRIC RELATIONSHIPS

Michael E. Montgomery

Research Entomologist, USDA Forest Service
Northeastern Forest Experiment Station
Center for Biological Control of
Northeastern Forest Insects and Diseases
Hamden, Connecticut 06514

Spruce budworm larvae grew faster than gypsy moth larvae both in a temporal and relative sense. The budworm larvae had a higher relative growth rate (RGR), biomass conversion efficiency (ECI), and nitrogen utilization efficiency (NUE) than the gypsy moth larvae. As both species matured, relative growth rates, rates of consumption, and conversion efficiencies declined.

The differences between species and the decline in rates with maturation are, at least partially, allometric (related to body size). The relationship can be expressed by the equation $y = aX^b$, where y is the rate of the process and X is the size of the animal. The importance of accounting for allometry when evaluating quantitative nutritional measurements is illustrated with budworm and gypsy moth.

INTRODUCTION

This paper will examine growth of the spruce budworm *Choristoneura fumiferana* (Clemens), and the gypsy moth, *Lymantria dispar* L., each on a representative host plant. The emphasis of the study was to obtain a better understanding of the basic nutritional physiology of caterpillars, particularly in regard to changes associated with size and/or age, rather than to examine effects of food quality on caterpillar growth.

Size attained, e.g., pupal weight, is a parameter frequently used to assess the effect of host nutritional quality on insect performance. While size measurements illuminate the extent to which an insect grows on a particular food source, they do not provide information as to why a food is superior or inferior. For example, poor growth can be the result of lowered consumption due to the absence of a phagostimulant or the result of lowered food utilization due to the presence of a toxic chemical.

The quantitative nutritional approach of Waldbauer (1968) provides a method to answer such questions. This involves measuring food consumption, excretion, and assimilation and calculating utilization and efficiency rates. The effect of insect size, e.g., absolute weight, on these nutritional indices has often been overlooked by entomological researchers.

Definitions

Terminology used in this paper is patterned after that of Waldbauer (1968):

$$G = I - E - R,$$

where G = growth (biomass gained), I = food ingested (consumed), E = excretion (feces) which includes both undigested food and metabolic waste, and R = respiratory loss from metabolism.

These values, which are expressed as dry weight, can be converted to relative rates by dividing the absolute value by the elapsed time period (Δt) and the mean weight (W) of the animal during the time period. Unfortunately, authors define mean weight according to their personal whims. Some use a simple average of the initial and final weight whereas others calculate an exponential mean based on initial and final weight. There are several methods used to do the latter. When daily or several measurements are made between the time interval, mean weight is often approximated as the sum of the individual measurements divided by the number of measurements.

Waldbauer (1964) made daily measurements and calculated mean weight by summing daily weights, after adjustment of the initial and final weights, then dividing by total number of days. This method approximates a solution by integrals. I have noted that several authors who measured only the initial and the final weight cite Waldbauer for method of calculating relative rates. What was done in these cases is unclear since Waldbauer's method is applicable only for a series of several measurements that can approximate a continuous record. Waldbauer's (1964) growth rate (GR) does not necessarily describe a true growth rate. Kogan and Cope (1974) show how this rate differs from the mean relative growth rate ($\overline{RGR}$) (Radford 1967) employed by general physiologists.

Herein, mean weight is defined as:

$$\overline{W}e = W_f - W_o/\ln(W_f/W_o)$$

where W_f = body dry weight at the end of the period, and W_o = body dry weight at the start of the period. Relative rates for biomass, then, are

Relative Consumption Rate (RCR) = $I/\overline{W}_e/\Delta t$

Relative Growth Rate (RGR) = $G/\overline{W}e/\Delta t = \ln W_f - \ln W_o/\Delta t$

Budgets and relative rates for nitrogen can be calculated in much the same manner as for dry matter biomass. It is assumed that nitrogen is not eliminated by the insect in gaseous form; hence, the nitrogen budget can be expressed as:

$$G(N) = I(N) - E(N),$$

where nitrogen gain G(N) in the insect body is the difference of nitrogen ingested I(N) and nitrogen excreted E(N). Relative rates for nitrogen are:

$$\text{Nitrogen Accumulation Rate (NAR)} = G(N)/\overline{W}_e/\Delta t$$

$$\text{Nitrogen Consumption Rate (NCR)} = I(N)/\overline{W}_e/\Delta t$$

$$\text{Nitrogen Excretion Rate (NER)} = E(N)/\overline{W}_e/\Delta t$$

The usefulness of relative rates is that they facilitate comparison between diets, instars, and species. Food utilization indices, expressed as percentages or ratios, are also useful in making comparisons. Utilization indices used herein are:

$$\text{Ingested matter efficiency (ECI)} = \frac{G}{I} = \frac{RGR}{RCR}$$

$$\text{Nitrogen efficiency (NUE)} = \frac{G(N)}{G(N)+E(N)} = \frac{NAR}{NCR}$$

Rearing and Data Collection

Gypsy moth larvae were reared individually from neonate to pupation on excised foliage of red oak, *Quercus rubra*. Foliage was changed at 48-hr intervals and kept turgid by placing the leaf stem or twig in a vial of water. Larvae were placed on the foliage about one week after budbreak and maintained at temperatures that approximated outdoor weekly mean temperatures. Eight to twelve of the larvae were sacrificed at the beginning of each instar just after hatch or the molt before any feeding occurred. The dry weight of the insect body including the newly molted larval skin, and the feces produced during the instar were measured. Standard micro-Kjeldahl procedure was used to find the nitrogen content of larvae and feces and the percent nitrogen of freeze-dried subsamples of the foliage provided the larvae at each feeding. Nitrogen ingestion was calculated as the sum of G(N) and E(N). Dry matter ingestion was calculated as I(N)÷N/mg foliage.

Spruce budworm larvae were reared on artificial diet until mid third instar at which time they were placed individually on a single terminal bud of balsam fir, *Abies balsamea* that had just shed the scale cap. They were maintained outdoors in a weather station box at ambient temperature. Humidity in the 28 ml plastic rearing container was at or near 100% RH. Larvae were divided into two groups: those that were sacrificed periodically to obtain dry weight and nitrogen content as percent of wet weight, and the experimental group reared to pupation. For the latter group, foliage was changed, frass separated from foliage and larval wet weight measured at 48-hr intervals. Larval dry weight biomass was estimated from the wet weight times the dry/wet weight ratios of larvae of corresponding size. This value was reduced 20% to account for gut contents except for larvae ready to enter the prepupa stage. Dry weight or N consumption of foliage was estimated by (1) counting number of needles damaged (completely or partially consumed) and measuring length of uneaten portions and (2) determining mean length ($\overline{x}$ L), dry weight, and nitrogen content of undamaged needles from the same twig which was used to calculate needles eaten as:

$$\frac{((\#\text{ damaged needles})\text{x}(\overline{x}\text{L}))-(\text{total uneaten length})}{\text{mean length}}$$

Thus:

I = needles eaten x mean wt/needle
I(N) = needles eaten x mean N/needle

Results and Discussion

Table 1 compares spruce budworm and gypsy moth weight, development time, fecundity and conversion efficiencies. For the sake of convenience and brevity, only the data for females are presented throughout the paper. The budworm increased body weight about 2000-fold and the gypsy moth nearly 3000-fold; but the gypsy moth took 50% longer to complete development. In effect, the gypsy moth achieved a greater absolute percentage increase in size, but did so at a slower rate of growth (RGR). The gypsy moth also fed less efficiently than the budworm both in terms of dry matter and nitrogen. This may have contributed to the lower RGR of the gypsy moth, however; as will be pointed out the difference in rate could also be explained by size differences.

The RGR, ECI, and NUE values, as presented in Table 1, represent averages for the entire larval period (*L. dispar*) or for the third instar until pupation (*C. fumiferana*). It is common practice to make measurements across instar or the entire larval stage and to express the results as a constant value independent of absolute body weight. This is an arbitrary simplification that fosters the idea that rate of growth and food conversion efficiency remain unchanged as the larva grows. In reality, such rates and indices are not constant as the animal grows but change, usually in a systematic manner with time or the weight of the insect. It would seem, therefore, that a parameter which depicts change in rate (=slope) would be as useful as mean relative rate.

Table 1. Bionomic data for female larvae

Insect Host	*C. fumiferana* Fir	*L. dispar* Red Oak
Initial dry weight (ug)	18	140
Pupal dry weight (mg)	30	400
Development time (days)	30	48
Relative growth rate (μg/mg/ °day)	15.6	11.1
Biomass conversion efficiency (%)	9.1	6.6
Nitrogen utilization efficiency (%)	40	30

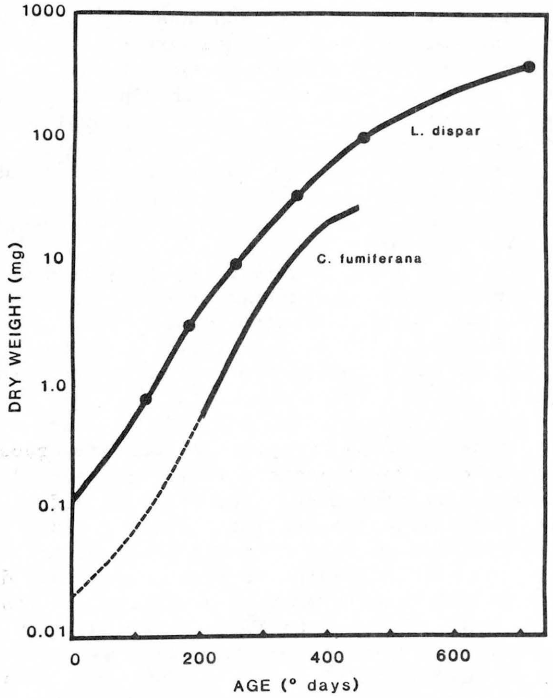

Figure 1. L. dispar and C. fumiferana growth against time. Measurements for L. dispar were made at each instar molt; for C. fumiferana every 2 days beginning at 200 degree days, the dashed line is an extrapolation.

It is also common practice to plot against time the log weight of the developing organism (Fig. 1). An easy and frequently used method to mathematically describe such growth is to regress the logarithm of the weight on time. This type of regression is appropriate if growth was exponential; i.e., weight increases at a constantly increasing rate until death or metamorphosis interrupts the process. If the growth of the two caterpillars was exponential, the data sets plotted on a log linear scale, as in Figure 1, would produce a straight line. The growth curves though are clearly sigmoid; i.e., the weight increases exponentially but with a rate of increase that changes with time. Curves used to describe this type of growth are, among others, the power, Gompertz, logistic, and Bertalanffy (Kaufman 1981).

The Bertalanffy equation has been used to describe the growth of plants, fish, mammals, and humans. It can can be written as:

$$dW/dt = {}_{n}W^{a} - {}_{k}W \qquad (1)$$

where W = weight, t = time and a, k, and n are parameters.

A closed form solution of this equation is:

$$W = \left[\frac{n}{k} - \left(\frac{n}{k} - W_o{}^{(1-a)t}\right) e^{-k(1-a)t}\right]^{1/1-a}$$

where W_o = weight at time, t=0. Needless to say, fitting this and other nonlinear models to data requires knowledge of calculus and matrix algebra and a computer programmed to do a nonlinear least-squares analysis. Such process is beyond many while to others proposing plausible equations and seeking "the" formula that most closely approximates the experimental data is great mental sport. The goal however should not be to achieve high statistical fit via complex equations but to describe and use data in a manner that facilitates evaluation of effects of substrate and environment on the growth process.

Graphical plots are a convenient, straightforward method that allows one to describe changes in growth rate as a function of size.

Figure 2 shows that body size and RGR of L. dispar and C. fumiferana are allometric functions. With both species, the log of RGR more or less decreased in direct proportion to the log of the weight. Although the overall RGR of the budworm was higher than that of the gypsy moth, it was more sensitive to size and decreased at a faster rate as the larvae grew.

The initial value for L. dispar represents the first larval stadium and may underestimate RGR. L. dispar neonates normally spend the first 24-48 hours wandering and not feeding; a period of dispersal. To account for this, the time interval for the stadium was shortened 17 degree-days which may have been insufficient. On the other hand, the first instar RGR may actually be lower since the larva must replenish the moisture and energy expended during the nonfeeding interval before a net increase can occur.

The greater fluctuation of the C. fumiferana data about the regression line reflects the higher variability in measurements for this species. Standard errors of budworm larval weight and consumption ranged from 10-20% of the mean whereas gypsy moth standard errors were always less than 10% of mean values.

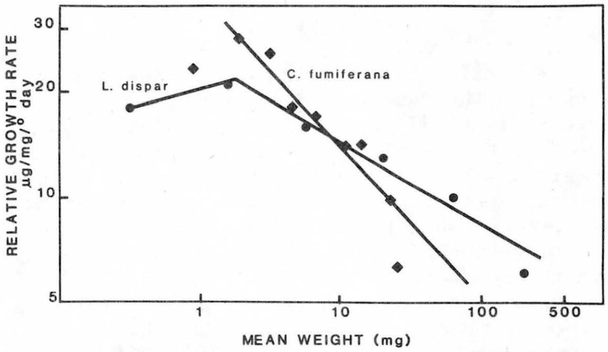

Figure 2. Relative growth rate (RGR) of L. dispar and C. fumiferana against mean weight ($\overline{W}_e$).

The relationship between metabolic rate and absolute body size is one of the classical topics of comparative physiology. That the normal or basal metabolic rate of plants and homeothermic and poikilothermic animals is inversely related to body size; i.e., smaller organisms have higher metabolic rates, is something learned by introductory biology students (Keeton 1972). This relationship can be approximated by allometric formula (Huxley 1932):

$$M = {}_{b}W^{\alpha} \qquad (2)$$

where M = metabolic rate per unit of time, W = body weight, and α and b are constants. For weight-specific metabolic rates, the equation becomes:

$$\frac{M}{W} = {}_{b}W^{\alpha-1} \qquad (3)$$

On a log-log graphical plot, an empirical data set that follows this function would afford a straight line regression, the slope of which indicates α. If $\alpha = 2/3$, then the surface rule is being followed; i.e., the change in rate decreases in proportion to the change of surface area. If the slope is 45°, $\alpha = 1$, then change in rate is directly proportional to the change in weight. Bertalanffy (1957) has proposed that metabolic rates of most animals are proportional either to surface area, to weight, or, more rarely, lie between these two types. Brody (1945) however, indicated that basal metabolic rate varies at the 3/4 power of weight. Most laboratory measurements are close to this value (Fenchel 1974).

It is not unreasonable to assume that rules similar to those regarding the size dependency of metabolic rates would extend to growth rates. After all, is not growth in its simplest terms but the product of anabolism minus catabolism? Adolph (1949) showed that, at least in first approximation, the rate of all physiological processes can be expressed as allometric formulae. Thus, change in body weight can be expressed as a function of the difference between building up and breaking down; i.e.:

$$dW/dt = {}_{n}W^{a} - {}_{k}W^{b}$$

This is similar to the Bertalanffy equation except for the addition of parameter b. Bertalanffy (1957) in developing his equation argued that catabolism is directly proportional to weight and since the basic equation is rather insensitive to minor deviations in b, it can be regarded as equal to one. The exponent a then more or less depicts the relationship of growth rate to body weight.

Less predictable is the effect of body size on food consumption rates and food conversion efficiencies. Food consumption would be expected to be proportional to body weight if the insect simply feeds to repletion once or twice daily. In this case, digestive efficiency would likely decrease with increasing body size, since gut surface area decreases at about 2/3 power of gut volume. Conversely, if digestive rate rather than gut volume delimits the rate of food consumption, one would expect digestive efficiency to be rather independent of body size and consumption to be more proportional to surface area than to body volume. Food conversion, however, is not just digestion but also intermediary metabolism plus several complex and intertwined physiological and metabolic processes and thus it is difficult to predict what type of model would fit. The final net result however is measurable and can be tested for size dependency.

Figure 3 plots logarithmically RGR as well as several other nutritional indices. The regression lines are fitted by eye and approximate. The plot is intended only to illustrate the relationship of the general trend of the indices to each other.

With *L. dispar* (Fig. 3a), RCR followed the same pattern as RGR except that RCR decreased at a slower rate as size increased. Consequently, ECI (Fig. 3c) decreased. The nitrogen budget (Fig. 3b) followed a similar pattern. NAR decreased at a steeper rate than NCR; hence, NUE (Fig. 3c) also decreased as size increased. Note that the NER changed much less with weight than either NAR or NCR. Both NUE and ECI had about the same slope; an indication that they were not affected differentially.

The *C. fumiferana* data are more complex. They are also less precise; hence, interpretation must be taken lightly. In this case, RCR decreased but then began to increase as pupation neared while RGR changed at a constant rate (Fig. 3d). NCR exhibited a similar pattern even though NAR decreased continuously as size increased (Fig. 3e). NER was apparently little affected by larval size. Since RCR and NAR decreased at a decelerating rate and rate of decrease of RGR and NER remained constant, ECI and NUE decreased at an accelerating rate (Fig. 3f).

My starting hypothesis was that since RGR is affected by weight, RCR and ECI would also be influenced by weight since RGR = RCR x ECI. Indeed, a general pattern was observed where growth, accumulation, and efficiency decreased as body size increased. However, each index had a different slope which indicates independent influence and/or compensation mechanisms.

Rate/efficiency interactions involve the complex area of feedback and homeostasis and is an area largely unexplored by insect physiologists. Slansky and Feeny (1977) proposed that rate of growth or accumulation is held stable, maximal, by compensatory changes in consumption and efficiency. Their data supported the hypothesis of Odum and Pinkerton (1955) that power and efficiency cannot be maximized simultaneously and that power (i.e., assimilation rate) would be selected for.

An examination of the regression coefficient of the indices (Table 2) for *L. dispar* not only supports the thesis that power or accumulation rate is stabilized at a high rate but also offers an explanation why efficiency decreases as size increases. The reason for suggesting that *L. dispar* RGR and NAR are maximal is that the constant of proportionality, a-1, was very close to the 3/4 power rule for metabolic rate. In other words, the caterpillar's accumulation of biomass and nitrogen changed at the theoretical, expected rate despite changes in food supply. (Effect of food will be discussed later.)

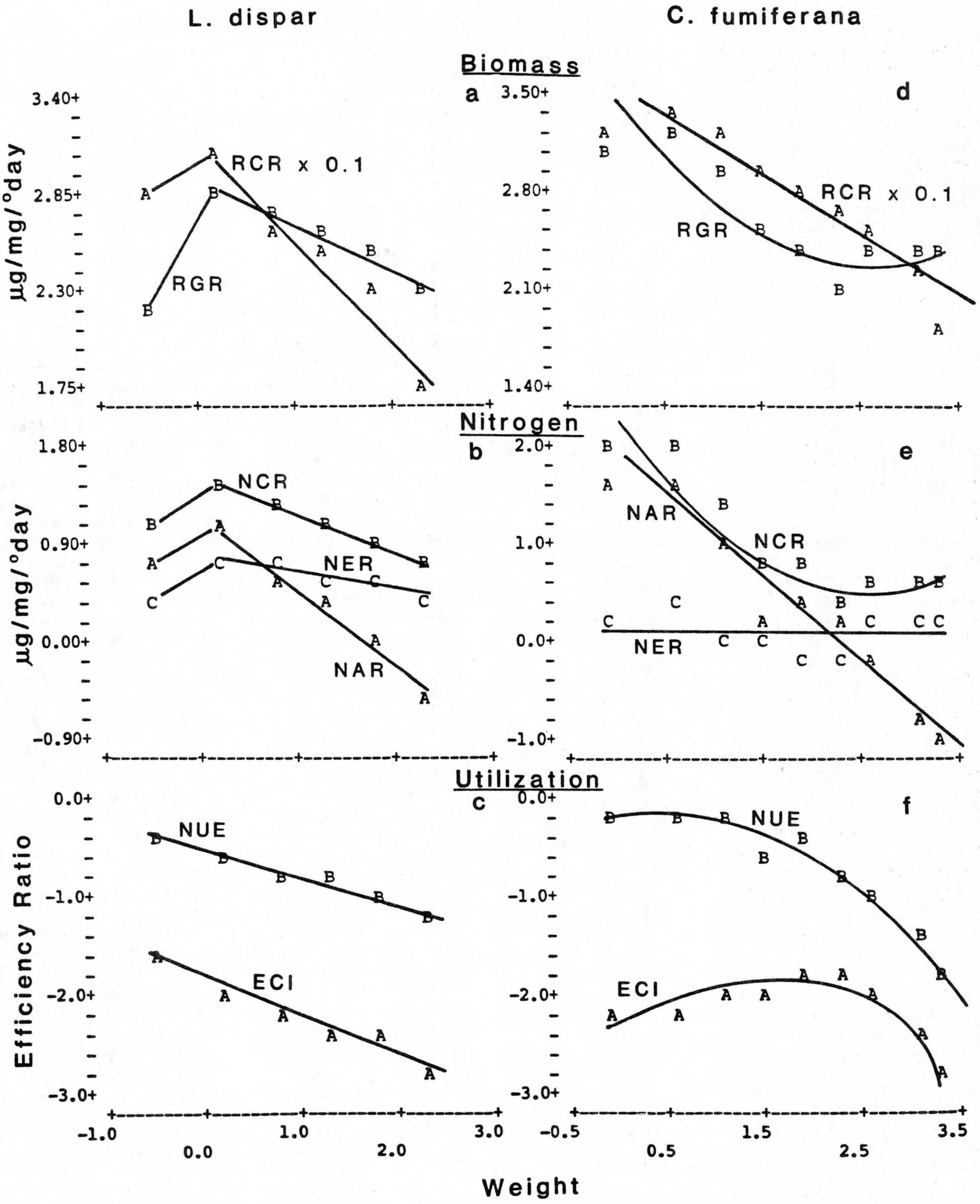

Figure 3. Weight dependency of nutritional indices. Values have been converted to natural logarithms. (See Definitions section for abbreviations.)

Table 2. Regression equations and coefficients of determination of nutritional indices on log $\overline{We}$. The equations have the form: log (index) = a log $\overline{We}$ + log b. (Index units = µg/mg/°day, weight = mg).

	L. dispar			*C. fumiferana*		
Index	b	a-1	r^2	b	a-1	r^2
RCR	182.6	0.90	0.94	236.1	0.69	0.71
RGR	25.2	0.75	0.97	31.4	0.62	0.81
NCR	4.7	0.85	0.99	6.6	0.53	0.76
NAR	2.8	0.73	0.96	6.2	0.18	0.93
NER	2.1	0.93	0.97	0.5	-0.71	0.38

Consumption and excretion also seem to be following ideal case models. These indices are fairly close to one and hence more directly proportional to volume (= weight) compared to accumulation where direct proportionality is closer with surface area ($A = V^{2/3}$). Since gut volume is roughly proportional to body volume (= weight), then a proportionality constant for RCR of near zero (0.9 - 1 = -0.1) indicates the insect eats to repletion. Assimilation of the food however proceeds only at the 3/4 power of the rate of intake; hence, assimilation efficiency decreases as intake increases. This scenario implies little feedback control over feeding rate, the insect simply eats until it is full if food is available and palatable.

The data suggest an intriguing, alternative scenario. Catabolism is also weight proportional (cf. *L. dispar* NER) and responds more to weight change than anabolism (Bertalanffy 1957). This fact also can explain size related decrease in efficiency. Further, if catabolism and/or elimination of metabolic waste were rate limiting, it, through feedback, could control feeding rate. An excess of nonutilizable metabolites that must be eliminated would depress feeding rates. Better assimilation efficiency would result in faster growth not only from the increased conversion, but also from an increase in consumption the production of less wastes would afford.

These remarks about rate/efficiency interactions are pure speculation. Its purpose is more to illustrate the caution required and the difficulty in relating indices to performance or to cause and effect.

The spruce budworm data in Table 2 were ignored in the preceding discussion because the data apparently illustrate effect of substate more than ontogeny. The budworm proportionality constants were lower than expected and suggest that phenological changes in the fir foliage placed increasing stress on the budworm as it matured. On the other hand, the gypsy moth data seem to reflect mainly a scaling effect. One would need to suppose that young oak foliage was relatively less suitable than older foliage or that the lower early season temperatures were more favorable in order to account for a phenological effect on the gypsy moth constants.

To illustrate phenologic relationships between foliar chemistry and the indices, I have plotted some of my unpublished foliar analyses on logarithmic axes with the corresponding mean larval weight substituted for sample date on the axis of the abscissas (Fig. 4). Significant correlations of chemical levels with nutritional indices are almost a foregone conclusion simply because the indices decline with size (time) and most of the chemicals either increase or decrease in concentration with time. Because of the overbearing effect of allometry, few of these correlations can be rationalized. For example, condensed tannin in oak leaves increased as the leaves matured whereas in fir tannin decreased after budbreak. In the first case, the correlation coefficient with RGR is -0.96 and in the second, 0.99. Total phenol in oak is obviously poorly correlated with RGR, but it cannot be ruled out that total phenol was without influence if the change in RGR is mainly ontological.

The situation with nitrogen seems more informative. Budworm RGR and NCR were strongly correlated, 0.96 and 0.99, respectively, with foliar nitrogen. Budworm development was rapid and closely synchronized with foliar expansion. The larvae were in 3rd instar at budbreak and pupation occurred as the foliage became fully expanded and nitrogen level stabilized. With oak, leaf expansion was completed and nitrogen level stabilized when the gypsy moth larvae were about half grown. In this case, correlations of nitrogen with RGR and NCR were less, about 0.7.

Nitrogen in mature fir foliage may have been limiting to budworm since it was below 1.5%. Oak, by contrast, had 2.3% N in mature foliage. It would seem to be advantageous for the budworm to complete development before the foliage matures. Both its habit of attacking foliage before buds break and its small size may be adaptations that aid this. Decline in growth rates with increasing size occurs also among species, i.e., small animal species tend to have higher RGR (Schmidt-Nielsen 1975). McNab (1978) stated that herbivores of equal size feeding on woody foliage have significantly lower metabolic rates than those feeding on richer plant tissues. The budworm gypsy moth comparisons do not support this. (See Mattson 1980 for more on body size.)

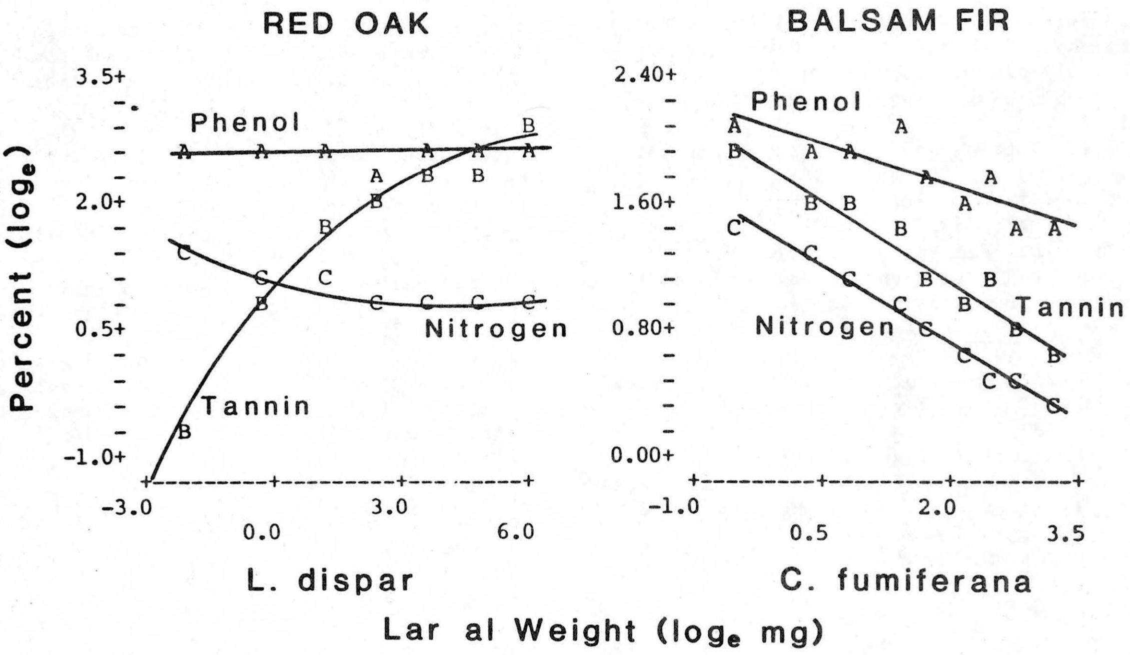

Figure 4. Seasonal change in concentration of foliar chemicals in relation to larval weight at time of sampling. Values have been converted to natural logarithms.

Gypsy moth is a rather large caterpillar with a rather long development time for a spring-feeding arborivore. Speed may have been sacrificed to efficiency (Fig. 5). Budworm by contrast had higher NUE on spruce where growth was less. The plants that supported poor budworm growth also had lower foliar nitrogen levels (Montgomery, unpublished). This observation complements the data for developing larvae (Figs. 3 and 4) where, as nitrogen became in apparent critical supply, NUE decreased more than expected while NAR was maintained. Both host and development data for budworm support the thesis of Odum and Pinkerton (1955) that efficiency is of lesser importance than rate. It should be clarified that although changes in RGR due to size applies to different sized individuals, species, etc., there is no evidence (see Banse 1979) that the weight (= age) dependent efficiency that occurs in a growing individual applies to individuals of different size. Thus, the size/efficiency relationship of budworm in Figure 5 may or may not be allometric.

Although firm statements about the weight dependency of nutritional indices cannot be made, that such effects may exist is sufficient reason to consider the role of allometry when interpreting quantitative nutritional data.

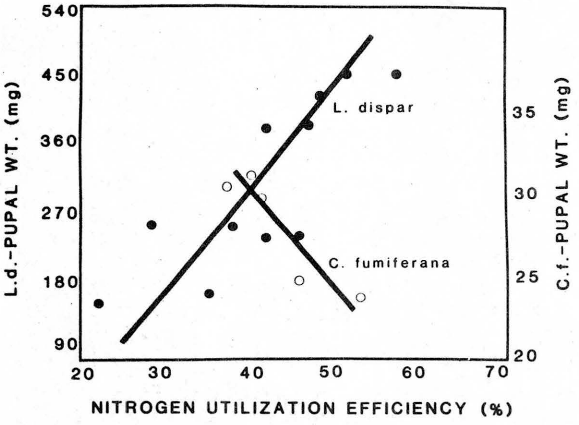

Figure 5. Mean nitrogen utilization efficiency against mean female pupal weight for L. dispar (L.d.) on eleven different host species and for C. fumiferana on white spruce hosts differing in age and vigor (Montgomery, unpublished).

Acknowledgement

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SUMMARY REMARKS

Many of the papers presented discussed foliage chemistry and/or the response of caterpillars to dietary chemicals. The concluding two papers, one by Houston on characteristics of stands resistant and susceptible to defoliation by gypsy moth, and the other by Witter et al. on management implications of budworm/host interactions, do not discuss foliage chemicals or foliage quality per se. Instead, they focus on traditional site classification systems. More than anything, this is indicative of where the "state-of-the-art" is and the gaps in knowledge that future research should fill.

Forests have traditionally been classified as to physical and phytosociological characteristics such as soil, slope, species composition, stocking density, and tree age. Because of their familiarity to the forest manager and their relative ease of measurement, they are the characters currently being incorporated into site classification schemes. Such entities are a step removed from the actual cause-effect relationship. They act on the physiology and growth habit of the host tree (the "room and board" referred to in the paper by Wallner) which in turn influences pest insect populations. The quality of the "board", at its lowest denominator, is determined by the chemicals used as food and anything that affects the ability of the insect to access or utilize them.

Research at this level may seem distant to practical payoffs. The papers presented indicate both the progress and challenges of such work. The introductory chapter by Talerico cited that a relationship between budworm growth and natural variation in foliar components had not been previously demonstrated. Papers given by Wagner and Blake, Montgomery, Mattson et al., and Schmitt et al., noted a positive correlation between budworm pupal or adult weight and concentration of foliar nitrogen. The importance of nitrogen did not extend to the gypsy moth. Lechowitz found little correlation between foliar N levels and gypsy moth host preferences and Montgomery reported a similar situation with pupal weight. The latter author did report, though, that nitrogen utilization efficiency was highly correlated with gypsy moth pupal weight. Apparently something, perhaps tannins, inhibited utilization of the foliar nitrogen. Of the several papers that presented data on tannin or phenolic foliar levels, none reported strong evidence of a negative effect on budworm or gypsy moth. Schultz and Baldwin explained however that it may not be the "mean" level of secondary chemical in the tree, but the induction or increase in concentration in response to insect attack that is important. Thus, foliage quality should not be considered as static, but dynamic and variable, not only in time, but also in space. This presents sampling problems not only to the insect, but also to the researcher. The models presented by Valentine and Fleming showed that lowering of foliage quality may not necessarily be beneficial from a pest management standpoint for populations may be prolonged at high levels instead of crashing because of starvation.

I must chide myself as well as this symposium for focusing excessively on foliage chemistry. Many other aspects of the host insect interaction such as Shepard's paper on bud phenology were also discussed. But perhaps the greatest imbalance was the focus on identifying mechanisms responsible for host suitability without documenting their action in the field under natural conditions. The second paragraph of the paper by DeHayes comments well on this.

August 1983 Michael E. Montgomery, Hamden, CT

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Proceedings, forest defoliator--host interactions: A comparison between gypsy moth and spruce budworms; 1983 April 5-7; New Haven, CT. Gen. Tech. Rep. NE-85. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; 1983. 141 p.

Fosters communication between researchers with active research projects designed to understand the relationships between the host plant and forest defoliator feeding behavior, growth, and reproduction.

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- Parsons, West Virginia.
- Princeton, West Virginia.
- Syracuse, New York, in cooperation with the State University of New York College of Environmental Sciences and Forestry at Syracuse University, Syracuse.
- University Park, Pennsylvania, in cooperation with the Pennsylvania State University.
- Warren, Pennsylvania.

Forest Defoliator – Host Interactions: A Comparison between Gypsy Moth and Spruce Budworms